Review Article

A Review of Hypothesized Determinants Associated with Bighorn Sheep (*Ovis canadensis*) Die-Offs

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Multiple determinants have been hypothesized to cause or favor disease outbreaks among free-ranging bighorn sheep (*Ovis canadensis*) populations. This paper considered direct and indirect causes of mortality, as well as potential interactions among proposed environmental, host, and agent determinants of disease. A clear, invariant relationship between a single agent and field outbreaks has not yet been documented, in part due to methodological limitations and practical challenges associated with developing rigorous study designs. Therefore, although there is a need to develop predictive models for outbreaks and validated mitigation strategies, uncertainty remains as to whether outbreaks are due to endemic or recently introduced agents. Consequently, absence of established and universal explanations for outbreaks contributes to conflict among wildlife and livestock stakeholders over land use and management practices. This example illustrates the challenge of developing comprehensive models for understanding and managing wildlife diseases in complex biological and sociological environments.

1. Introduction

Effective management and conservation of wildlife populations can be undermined by multiple causes. These include decreased and altered habitat and other direct anthropogenic effects, climate change, competition and predation from nonnative wildlife and domestic species, demographic challenges associated with small populations, multiple, incompatible management objectives for sympatric species or their habitat, and exposure to native and exotic infectious agents [1–4]. The consequences and interactions of these variables are difficult to understand and predict, and may vary by circumstances. This uncertainty, particularly when it occurs in

complex sociological environments where stakeholders have differing values and objectives, presents substantial challenges for decision makers. In such uncertain environments, the absence of data and differing values can result in polarized debate among stakeholders. It can also serve as an impediment to the acquisition of data that would contribute to effective management. Respiratory disease outbreaks in bighorn sheep (*Ovis canadensis*) illustrate the challenge of identifying and managing disease in valued wildlife populations, where stakeholder perceptions and values clash [5].

Bighorn sheep are highly valued for recreational, ecological, philosophical, spiritual, and other reasons [6]. Bighorns have experienced a population decline of two orders of

magnitude subsequent to 19th century settlement of western North America [7]. This decline has been attributed to a combination of human activities, such as overhunting, domestic livestock grazing, introduced infectious agents, and displacement from range and migratory paths. While translocations and other management activities have resulted in partial recovery of populations and numbers, die-offs have seriously undermined bighorn sheep recovery efforts [8]. Moreover, uncertainty regarding the agents, reservoirs, and causes of outbreaks has contributed to stakeholder polarization [5, 9]. Recent die-offs at multiple locations during the winter of 2009-2010 highlight the need to identify causes and potential management strategies for respiratory disease outbreaks in bighorn sheep [10].

Research to date has largely focused on identifying an agent and reservoir responsible for causing bighorn die-offs. Early research on bighorn respiratory disease die-offs focused on lungworm-pneumonia complex, due to protostrongylid lungworms (*Protostrongylus* spp.) that are likely indigenous parasites of bighorn sheep and other free-ranging caprines [11, 12]. More recent research has focused largely on Pasteurellaceae with the hypothesis that domestic sheep (*O. aries*) serve as reservoirs for an infectious agent or agents that is (are) fatal in bighorn sheep, as well as in response to policy-driven arguments against this hypothesis [13–16]. However, placing research on agents and reservoirs in context is difficult, particularly for data collected under captive conditions. One contextual challenge is the inconsistency in agents associated with different outbreaks [17–19]. In addition, contrasting models of transmission have been proposed. Some outbreaks subjectively appear to be propagated epidemics [19, 20], possibly due to a single, novel infectious agent that was recently introduced into a population. In contrast, web of causation [21] models represent a more holistic perspective that considers multiple environmental, host, and agent determinants of disease and their interaction. Web of causation models are similar to those accepted for domestic livestock models of “shipping fever” [22–26], and leave open the potential for endemic agents to cause outbreaks with certain combinations of determinants. The potential for endemic agents to favor outbreaks, or to sporadically cause increased morbidity or mortality that is perceived as an outbreak, has been less considered than the introduction of novel agents to naïve populations. Resolution of these issues, in part, will contribute to development of management strategies and resolution of contention regarding land management policies for domestic and bighorn sheep. Full resolution will likely require sociological approaches to resolve differing values for land use among stakeholders.

The objective of this paper is to critically consider the relative role of various factors in limiting bighorn sheep populations, with an emphasis on outbreaks and infectious agents. Since there is uncertainty as to whether endemic agents can sporadically cause outbreaks, this review will first consider environmental and host determinants of disease. This broad-based approach also helps to place the impact of infectious disease in context with other population-limiting factors. It will not be assumed that these determinants are temporally and spatially constant. This approach is consistent with the

TABLE 1: Causes of direct mortality proposed to limit free-ranging bighorn sheep populations.

Cause of direct mortality	Geographic distribution of determinant	Locations where determinant reported	Selected references
Hunting	Range-wide	Range-wide	[27, 28]
		Alberta, Canada, and Montana	[29, 30]
		Arizona	[31, 32]
Predation	Range-wide	California	[33–36]
		Colorado	[27]
		Montana	[37]
		New Mexico	[38, 39]

use of multiple working hypotheses for scientific investigations [40]. Practical and sociological considerations that inhibit the resolution of biological questions will be acknowledged where relevant. While the available data does not support quantitative assessment of risk factors for die-offs, this paper can serve as a starting point for development of new approaches for addressing the challenge of bighorn sheep respiratory disease die-offs and management of infectious diseases in wildlife populations.

2. Determinants Limiting Free-Ranging Bighorn Sheep Populations

2.1. Direct Mortality. Historic and current causes of direct mortality serve as a point of comparison for mortality due to sporadic outbreaks, and their relative impact may change as circumstances vary. Causes of direct mortality to bighorn sheep include hunting and predation (Table 1). Hunting is considered a substantial cause of bighorn sheep population declines in the 19th and early 20th centuries [7]. Current regulations largely minimize mortality due to hunting, but must be responsive to changing conditions, due to the potential for localized or range-wide adverse impacts. Stakeholders are largely supportive of sustainable yields for bighorn sheep.

Predation has been a concern in several regions throughout bighorn sheep range (Table 1). Predation by puma (*Felis concolor*) may limit bighorn sheep in locations where predator populations are largely supported by sympatric native or domestic ruminant populations [33–35, 38]. It has been proposed that the impact may be greatest where pumas specialize on small populations of bighorn sheep [29, 30]. However, predation losses may be compensatory and may not generally limit bighorn sheep populations [41]. Indirect impacts of predation, such as predator avoidance behaviors, might predispose bighorn sheep to disease and die-offs, but this has not been established. Predator control programs could limit bighorn mortality in small, demographically vulnerable populations, where this strategy is acceptable to stakeholders.

2.2. Environmental Determinants. Environmental determinants are known to directly or indirectly affect the susceptibility of animals to disease [22] and have been proposed to

be limiting factors for bighorn sheep populations (Table 2). Combinations of extreme cold, heavy snow, or other adverse conditions may sporadically compromise bighorn sheep health and predispose to infectious disease die-offs, but are rare direct causes of mortality [42, 43]. Escape terrain is a temporally stable feature that probably characterizes where bighorn sheep can avoid predation and persist [44], but is unlikely to vary in space and time [45, 46]. In contrast, historic bighorn sheep range and migratory pathways to seasonal ranges are not temporally stable, due to anthropogenic activities [47, 48]. Regardless of whether physical environmental characteristics vary temporally or spatially or whether there are infectious disease concerns, understanding the impact of these characteristics on bighorn sheep carrying capacity is critical for designing management strategies for long-term persistence. There is a need to determine whether bighorn sheep populations at or below carrying capacity are less prone to outbreaks of disease.

Bighorn sheep carrying capacity is a dynamic function of food and water resources that vary seasonally and with weather patterns [49–52]. Recognition of this and its impact on animals is analogous to the basics of animal husbandry, where meeting animal food and water requirements is important for maximizing animal health and fecundity and minimizing disease. It is also a core wildlife management principle [1]. Proximity to free-standing water appears to be a good predictive variable for bighorn sheep in arid regions, much as provision of water represents basic animal husbandry [53]. However, the sequential hypothesis that increasing water availability will increase desert bighorn sheep carrying capacity, improve animal health, or reduce the risk of transmissible diseases has not been consistently supported [54–58]. Studies with small numbers of experimental units limit resolution of this issue, as do confounding variables that are inconsistently reported, including the quantity and timing of precipitation, amount of forage available, and forage water content. Development of artificial water sources represents a logical and potentially popular resolution to perceived conservation needs for bighorn, but confirmation of the relative risks and benefits is needed.

Precipitation's effect on the quantity and quality of forage available to bighorn sheep is a range-wide factor that can impact the nutritional health of bighorn sheep and sympatric species (Table 2). It has been reported that the quantity of forage available to bighorn sheep, recruitment, and carrying capacity are positively correlated with the quantity of precipitation [59–64]. Precipitation and forage production have been speculated to be proportionate to bighorn sheep resistance to disease [49, 65]. Furthermore, forage nutritional quality (i.e., digestible energy, protein, and minerals) varies spatially and with the timing of precipitation, and this may not coincide with bighorn sheep nutritional requirements at specific stages in their annual cycle. This is because plant community structure and the nutritional quality of different stages of plant growth vary based on when precipitation occurs during the growing season [60, 63, 66–68]. While little is known of bighorn sheep nutritional requirements, based on elk models [69], small differences in forage digestible energy that are not visibly detectable may affect bighorn

sheep fecundity and survival. These differences in digestible energy are likely intertwined with other nutritional requirements, such as those hypothesized for selenium, protein, and minerals [63, 70, 71]. An additional confounder is where forest succession or other advanced plant seral stages limit the presence of herbaceous plants [72, 73]. Greater clarity on the impact of precipitation on bighorn sheep forage quality and quantity may identify indices that can be used to identify periods of nutritional compromise, such as during periods of drought. These periods may represent times of increased risk for development of disease from endemic agents, or animal movements that favor increased exposure to novel agents. While precipitation cannot be managed, historical and predicted patterns can be incorporated into management plans, and strategies such as controlled burns [74–76] might be used to modify forage nutritional quality. However, the consequences of temporal variability in forage can be difficult to communicate. This may create obstacles to stakeholder acceptance of sporadic die-offs or other stochastic events that undermine achievement of management objectives.

Bighorn sheep nutrition can also be affected by competition for forage because of density-dependant effects from conspecifics and sympatric species (Table 2). Competition with domestic sheep is recognized for its potential to compromise long-term bighorn sheep persistence, especially in the context of climate change [77]. However, overgrazing by other domestic species, native ungulates, and high bighorn sheep populations have also been described in case reports for almost a century and in a recent computer simulation [3, 72, 78]. These effects may be seasonal, based on reports of adverse competitive effects that are specific to bighorn sheep winter range, yet have long-term impacts on population fecundity and mortality rates. Socially mediated competitive effects may also exist, based on reports of bighorn avoidance of domestic species under field conditions, and decreased maternal care and neonatal survival at high bighorn sheep population densities [59, 79–81]. Consequently, there is a need to quantify the carrying capacity and social impacts of multiple sympatric species on rangeland. Even where this information can be established, effectively addressing management interests that may conflict remains a challenge. For example, an agricultural enterprise could pose a threat to bighorn sheep health while concurrently preventing development of critical habitat used by bighorn sheep and other wildlife species [82]. Such dilemmas can be difficult to overcome for both biological and sociological reasons, particularly where viewpoints are polarized.

Environmental determinants of disease are well accepted as being relevant to animal health [22]. Consequently, it would not be surprising if there are environmental determinants of disease that favor bighorn sheep outbreaks. While some environmental determinants may be distributed throughout bighorn sheep range, spatial and temporal variation occurs. Understanding this variation may be useful for developing predictors of outbreaks or increased levels of chronic disease. Greater attention to the impacts of precipitation and inter-/intra-species competition on forage quantity or quality may reveal predictors that favor introduction of novel agents into bighorn sheep populations or outbreaks

TABLE 2: Environmental determinants proposed to limit free-ranging bighorn sheep populations.

Determinant (subcategories)	Geographic distribution of determinant	Locations where determinant reported	Die-off attributed to determinant ¹	Selected references
Adverse environmental conditions	Northern and mountain locations	California	Yes	[28]
		Colorado	No	[42]
		Canadian Rockies, Canada	Yes	[72]
		Wyoming	Yes	[43]
Escape terrain	Range-wide	Arizona	No	[83]
		Baja California Sur, Mexico	No	[84]
		Montana	No	[85]
		New Mexico	No	[44]
Range and migration restriction due to human settlement or activities	Range-wide	Alberta, Canada	No	[86]
		Arizona	No	[87]
		California	Unclear ²	[28]
		California	No	[88]
		Colorado	No	[27, 89–91]
		Colorado	Yes	[92] (also see [93])
		Montana	No	[94]
Free-water	Primarily arid regions	Desert, general	No	[95]
		Arizona	No	[96, 97]
		California	No	[54, 79]
		California	No	[53]
		Utah	No	[55]
<i>Food quantity</i>				
Limited forage and precipitation	Potentially range-wide	Alberta	No	[59]
		Arizona	No	[60, 98, 99]
		California	Yes	[65]
		Colorado	No	[61]
		Montana	Yes	[49]
		Nevada	No	[50]
		New Mexico	No	[44, 62]
		Texas	No	[63, 66]
		Utah	Yes	[51]
Plant community succession	Potentially range-wide	British Columbia, Canada	No	[73]
		California	No	[74, 75]
		Canadian Rockies, Canada	Yes	[72, 76]
		Montana	No	[94]
<i>Food quality</i>				
Protein deficiency	Potentially range-wide	Colorado	No	[27]
		Texas	No	[63]
Dietary mineral availability	Range-wide	Alberta, Canada	No	[100]
		Arizona	No	[60, 101]
		British Columbia, Canada	No	[102, 103]
		California	No	[28]
		Colorado	No	[27]
		Utah	No	[104]
		Wyoming	No	[105]
Selenium deficiency	Localized	Wyoming	Yes	[70]

TABLE 2: Continued.

Determinant (subcategories)	Geographic distribution of determinant	Locations where determinant reported	Die-off attributed to determinant ¹	Selected references
<i>Competition</i>				
Competition for forage-domestic species	Range-wide	Alberta, Canada	Yes	[106]
		Arizona	Unclear ²	[107]
		California	No	[28, 78]
		Colorado	No	[27, 89]
		Nevada	No	[108]
		Oregon	Yes	[109]
		Texas	No	[110]
		Wyoming	Yes	[111]
Competition for forage-bighorn sheep	Potentially range-wide	Colorado	Yes	[112]
		Montana	Yes	[113, 114]
		Tiburon Island, Mexico	No	[3]
		Wyoming	No	[115, 116]
Competition for forage-native ruminant species	Potentially range-wide	Canadian Rockies, Canada	Yes	[72]
		Colorado	No	[27, 89]
		Colorado	Yes	[112]
		Montana	Yes	[117]
		Montana	No	[94]
		Sierra Nevada, California	Unclear ²	[28]
		Wyoming	No	[118]
		Wyoming	Yes	[111, 113, 119]
<i>Seasonal</i>				
Competition for forage-limited winter range (environmental or nonspecific)	Potentially range-wide	Alberta and British Columbia, Canada	Yes	[120, 121]
		Colorado	No	[42]
Competition for forage-limited winter range (domestic livestock grazing)		Colorado	No	[4, 27]
Competition for forage-limited winter range (native ruminant species)		Wyoming	Yes	[122]
Competition for space (social impacts)	Potentially range-wide	Alberta, Canada	No	[59, 80]
		California	No	[79]
		Colorado	Yes	[19]
		Idaho	No	[81]

¹ Mortality considered to be in excess of baseline levels;² Mortality in excess of baseline versus endemic disease status was not clear.

from endemic agents. Consequently, there is a need to develop methods for evaluating bighorn sheep carrying capacity as it varies with time. An understanding of environmental determinants of disease will be required for development of management strategies that can respond to anthropogenic and climatic impacts on bighorn sheep habitat.

2.3. Host Determinants. Host determinants are known to directly or indirectly affect the susceptibility of animals to disease [22]. Knowledge of host determinants of disease for bighorn sheep is incomplete. These determinants can be

considered as extrinsic, such as previously discussed for nutrition, or intrinsic. Low variation in the major histocompatibility complex has been hypothesized as an intrinsic determinant that could result in a high susceptibility to infectious disease in bighorn sheep, but data does not support this hypothesis [123, 124]. Immune suppression due to elevated cortisol responses to external stressors has also been hypothesized to be an intrinsic determinant of disease [93]. However, standardized necropsy protocols for investigating the “stress” hypothesis have not been developed and applied to outbreaks. In addition, although noninvasive, antemortem evaluation of cortisol levels can be conducted with fecal assays,

few studies use this method to quantify the cortisol responses of free-ranging bighorn sheep to potential stressors [125, 126]. It is conceivable that elevated cortisol levels from rut activity could suppress bighorn sheep immune systems and be a determinant of disease for some outbreaks [43]. This is analogous to mortality and reduced resistance to disease in male *Antechinus stuartii*, a small marsupial, due to elevations in corticosteroids during the breeding season [127]. However, data on cortisol responses to rut, inter- and intra-specific interactions, anthropogenic activities, and other potential stressors is needed to fully evaluate the “stress” hypothesis. Such work will need to distinguish between cortisol responses, social behavior that facilitates transmission of infectious agents, and other host factors that may favor development of disease. Although little work has been done to establish host determinants as proximate or ultimate causes of outbreaks, identification of these determinants may provide a means of testing some hypotheses or as indices for identifying populations at risk of outbreaks.

2.4. Agent Determinants. Agents may act as primary pathogens, or cause opportunistic infections under some combinations of agent, environmental, or host determinants. A practical challenge that exists for identifying agent determinants of disease is their presence in both healthy and diseased bighorns [17, 18, 128]. A further challenge is the absence of consistently used definitions of subclinical infection and disease. Because baseline data is generally absent and logistic constraints can limit collection of useful diagnostic samples during an outbreak, it can be uncertain as to whether a given agent acts as a primary pathogen, an opportunistic pathogen, or is an incidental isolate. Primary pathogens are most likely to be novel agents that are introduced into a naïve population. If an agent causes opportunistic infections, it implies that the host is compromised due to other agent, host, and/or environmental determinants, and the agent may be endemic in the population. A corollary is that compromised hosts are also more vulnerable to developing disease from many agents. Agents that typically cause chronic or low-prevalence infections can be the cause of outbreaks if other determinants favor an increase in the prevalence and/or severity of disease. These distinctions are important because different management approaches may be needed to address the introduction of novel agents and opportunistic infections. It is also important to recognize that a given agent may not always be responsible for outbreaks or consistently act as either a primary or opportunistic infection, due to spatial or temporal variation, or the influence of other determinants.

2.4.1. Parasites. Bighorn sheep harbor a number of ecto- and endo-parasites [129]. Based on general animal models, these agents may act as primary pathogens or increase susceptibility to disease from other agents. Sheep scab (*Psoroptes* spp.) is an ectoparasite that has been reported range-wide and was first associated with bighorn sheep die-offs during 19th century settlement of bighorn sheep range [130–132] (Table 3). While early reports are consistent with the hypothesis that these outbreaks resulted from the introduction of novel

parasites to bighorn sheep, probably from domestic sheep, the ecology, reservoirs, and taxonomy of bighorn sheep *Psoroptes* spp. have not been fully resolved [133–135]. *Psoroptes* spp. is of interest to the livestock industry because it is a reportable agent, but infestations of domestic sheep may be subclinical, and clinical signs may be a function of an individual’s health status, reproductive stage, and immunity to the mites [136–138]. This may be similar in free-ranging bighorn sheep, where subclinical infestations, self-resolution of infestations without human intervention, and outbreaks associated with rut or drought conditions have been reported [139–142]. An outbreak, where high animal densities and drought were described, illustrates the challenge in distinguishing between compromised animal health due to competition for nutrition, density-dependent “stress” responses of the host, density-dependent transmission of an agent, and other factors [143]. However, in sum, these observations suggest that multiple environmental, host, and agent determinants may determine the clinical course of bighorn sheep *Psoroptes* spp. infestations. While it may be speculated that these determinants may also render bighorn sheep vulnerable to respiratory disease, a link between these two has not been established. Nevertheless, the potential for range-wide impacts and disease to be favored by changing conditions illustrates the importance of understanding how combinations of environmental, host, and agent factors may favor the transition from subclinical and/or low-prevalence disease to outbreaks.

Protostrongylus spp. (lungworm) are native endoparasites of bighorn sheep that are found range-wide, except under xeric conditions where gastropod intermediate hosts required for transmission are absent (Table 3) [144, 145]. *Protostrongylus* spp. have been associated with all-age die-offs (Table 3), and are also a source of summer verminous pneumonia in 3–6-w-old lambs [129, 146, 147]. Verminous pneumonia of lambs is the consequence of numerous L₃ larvae synchronously maturing in the lungs. However, all-age die-offs may be due to opportunistic bacterial infections that are secondary to lungworm lesions, based on isolation of multiple bacterial species from pneumonic lungs, histopathology, and recovery of lungworm from bighorn sheep without clinical disease [18, 27, 113, 148–150]. The absence of apparent disease in free-ranging bighorn sheep experimentally inoculated with *P. stilesi* and *P. rushi*, as well as observations of bighorn sheep with respiratory disease and low pulmonary burdens of lungworm, raises further doubt about the role of lungworm as primary pathogens [129, 151–154]. In addition, while the number of pulmonary lungworm present is correlated with precipitation, presumably due to favorable conditions for gastropod-intermediate hosts, lamb recruitment is also highest under such conditions [50, 59, 98, 148, 155]. This suggests that animals with good nutrition can moderate the effects of lungworm infections. Furthermore, while administration of anthelmintics is a logical response to lungworm infections, a study of multiple populations that used a crossover design indicated that this strategy is not efficacious for improving lamb recruitment in free-ranging bighorn sheep populations [156]. Thus, a simple, invariant relationship between lungworm and disease does not appear

TABLE 3: Infectious agent determinants proposed to limit free-ranging bighorn sheep populations.

Agent category	Infectious agent	Geographic distribution of determinant	Locations where determinant reported	Die-off attributed to determinant ¹	Selected references
Parasite	<i>Psoroptes</i> spp.	Range-wide	Arizona	Yes	[143]
			California	Yes	[28]
			Colorado	Yes	[27, 157]
			Montana	Yes	[130]
			Nevada	Yes	[130]
			New Mexico	Yes	[139, 158–161]
			Oregon	Yes	[109, 140]
			Texas	Yes	[110]
			Washington	Yes	[140]
			Wyoming	Yes	[118, 130, 131, 141, 162]
	Lungworm (<i>Protostrongylus</i>)	Range-wide in mesic habitats	Alberta, Canada	Yes	[163]
			California	No	[164]
			Colorado	No	[27]
			Colorado	Yes	[146, 165]
			Montana	Yes	[113, 166]
			Montana	No	[148, 167]
			Nevada	No	[168]
			Oregon	No	[149]
			Utah	No	[169]
			Wyoming	Unclear ²	[118, 122, 170]
	Lungworm (<i>Muellerius capillaris</i>)	Localized	Montana	No	[128]
			South Dakota	No	[171]
Bacteria	Pasteurellaceae	Range-wide	Alberta	Yes	[151]
			Arizona	No	[172]
			California	No	[164]
			Colorado	No	[27]
			Colorado	Yes	[19]
			Hells Canyon (Washington, Idaho)	Yes	[18, 152, 173]
			Idaho	No	[174]
			Montana	Yes	[17]
			Montana	No	[128]
			Nevada	No (endemic)	[175]
			Oregon	Yes	[176, 177]
			Wyoming	Yes	[43]
	<i>Arcanobacterium</i> (<i>Corynebacterium</i>) <i>pyogenes</i>	Presumed range-wide	Colorado	Yes	[157]
			Montana	Yes	[113, 166]
			Arizona	Yes	[178]
	<i>Mycoplasma</i>	Uncertain	Hells Canyon	Yes	[18, 179]
			Wyoming	Yes	[180]
	<i>Chlamydophila</i> (<i>Chlamydia</i>) <i>Psittaci</i>	Uncertain	Wyoming	Yes	[180]

TABLE 3: Continued.

Agent category	Infectious agent	Geographic distribution of determinant	Locations where determinant reported	Die-off attributed to determinant ¹	Selected references
Virus	PI3 ³ , RSV ⁴	Presumed range-wide	British Columbia, Canada	No	[181]
	PI ³ , BRSV ⁴	Presumed range-wide	Hell's Canyon	Yes	[18]
	PI3 ³ , BRSV ⁴ , BVD ⁵ , IBR ⁶	Presumed range-wide	Montana	Yes (some populations)	[17]
	PI3 ³ , RSV ⁴ , BVD ⁵ , IBR ⁶ , OPP ⁷ , BT ⁸ , EHD ⁹	Presumed range-wide	California	No	[164, 182, 183]
	PI3 ³ , BVD ⁵ , BT ⁸ , parvo virus	Presumed range-wide	Colorado and Wyoming	No	[184]
			Arizona, California, Idaho, Montana, Nevada, New Mexico, Oregon, Utah, Washington		
	RSV ⁴	Presumed range-wide	Colorado	No	[185]
				No	[186]
	BRSV ⁴ , BT ⁸ , EHD ⁹ , CE ¹⁰	Presumed range-wide	Arizona	No (EHD and BT isolated from 2 mortalities)	[60, 187]
	BT ⁸	Presumed range-wide	Trans-Pecos, Texas	No	[188]
	CE ¹⁰	Presumed range-wide	Alberta, British Columbia, Canada	No (high morbidity, but low mortality)	[189, 190]

¹ Mortality considered to be in excess of baseline levels;

² Mortality in excess of baseline versus endemic disease status was not clear;

³ PI3: parainfluenza-3 virus;

⁴ BRSV and RSV: bovine respiratory syncytial virus;

⁵ BVD: bovine viral diarrhoea virus;

⁶ IBR: infectious bovine rhinotracheitis virus;

⁷ OPP: ovine progressive pneumonia virus;

⁸ BT: bluetongue virus;

⁹ EHD: epizootic hemorrhagic disease virus;

¹⁰ CE: contagious ecthyma virus.

to exist for bighorn sheep. Consequently, other determinants, such as competition from high densities of bighorn sheep, native ungulates, and domestic livestock, may be factors predisposing to outbreaks [7, 113, 118].

Muellerius capillaris, a lungworm of domestic sheep that has become established in some bighorn sheep populations, may cause disease under some conditions [125, 171, 191]. Similar historic introductions in other settings have been recognized to be responsible for a mosaic landscape of native and introduced parasite species [192]. *Protostrongylus* spp. and *Muellerius capillaris* illustrate the challenges of discriminating between proximate and ultimate causes of disease, the importance of rigorous study design, the potential for nonnative agents to become established and cause disease in bighorn sheep populations, and the potential for agents responsible for clinically mild and/or low prevalence infections to contribute to outbreaks when favored by other determinants. Further, recent studies have indicated that the presence of dorsal-spined larvae in feces is not always indicative of infection by *M. capillaris*, but may involve L₁ (first stage larvae) of muscledworms, specifically *Parelaphostrongylus odocoilei* [191, 193]. Significantly, the potential of *P. odocoilei* as disease agents in free-ranging wild-sheep (thin

horn, *Ovis dalli*) has been demonstrated [194], although the extent of distribution for these parasites among populations of bighorn is undetermined.

Lungworm and muscledworms also illustrate methodological limitations that exist for agent surveillance in bighorn sheep [195–198]. Baermann analysis of feces has commonly been used as an antemortem, semiquantitative method for determining the number of L₁ per gram of feces (LPG) in bighorn sheep; standard analyses have now been superseded by the modification termed “beaker Baermann” which has superior recovery [199]. This approach is similar to fecal analyses of domestic livestock for endoparasite management in pasture environments [137]. However, whereas the domestic livestock parasites of interest have direct life cycles, lungworm and muscledworms have a gastropod intermediate host. Consequently, LPG is a poor index of transmission, as it requires temporally consistent fecal shedding of L₁, proportionate fecal L₁ infection and development to L₃ in gastropods, and proportionate consumption of L₃-infected gastropods by bighorn sheep to be predictive for parasite transmission. In addition, LPG has not been correlated with pulmonary lesions and is therefore not a valid index of body burdens of parasites [150, 155]. Another confounding factor

is that until recently, the L₁ of protostrongylids found in feces could not be definitively identified. Currently it is possible to separate all North American genera and species based on diagnostic molecular sequences (e.g., [200]). Use of LPG as an index of parasite “load” or as an index of transmission, however, does not have a strong biological basis, yet has been used in bighorn sheep parasitological studies due to an absence of alternative tools.

Scabies and lungworm illustrate agents with potential range-wide impacts on bighorn sheep. However, their role as proximate or ultimate causes of outbreaks may vary; they can be present without clinically apparent disease, yet may have a role in some outbreaks. This picture is further complicated by the concurrent presence of other parasites that may reduce animal’s resistance to disease (e.g., coccidia), or that cause localized morbidity (e.g., nose bot flies, *Oestrus ovis*) [89, 201–203]. In addition, parasites can serve as vectors for other infectious agents of bighorn sheep [204]. Consequently, parasite’s potential to contribute to outbreaks merits consideration, whether they are native agents, exotic agents, are intermittently reintroduced into populations, or are endemic. Parasites may be a particular concern for migratory populations that have become sedentary, due to the potential for high animal densities and/or extended exposure that favors transmission. In addition, other host-parasite systems illustrate the potential for climate change to result in expansion of parasite’s range or altered transmission dynamics [205–207]. Consequently, use of improved methodology and study design to identify host, environmental, and agent interactions is needed for the development of short- and long-term bighorn sheep management strategies.

2.4.2. Bacteria. Bacteria are commonly a component of respiratory disease in many domestic and nondomestic species. They can be either primary or opportunistic infections. Early reports hypothesized that bacteria were opportunistic infections of bighorn sheep that occurred when favored by host, environmental, or agent determinants [113, 157, 166]. This is similar to the shipping fever model of respiratory disease in domestic livestock. The shipping fever model views pasteurellosis as an opportunistic disease that results when endogenous Pasteurellaceae colonize the lungs of livestock compromised by different combinations of infectious agents, host and environmental determinants [23, 24, 208–210]. This model arose subsequent to the failure of single-agent experiments to provide an explanation for shipping fever. Recognition of the multifactorial nature of shipping fever resulted in the development of multiple, potentially concurrently used, management strategies to reduce its prevalence and severity in livestock.

The Pasteurellaceae are a heterogenous group that has experienced many taxonomic changes. A biovariant system of classifying Pasteurellaceae for wildlife work has been developed due to isolates that were not typable using conventional serologic classification systems [172], but utilization of genotype-based methods may be more appropriate for some research questions [211]. *Mannheimia haemolytica*, *Pasteurella multocida*, and *Bibersteinia* (formerly *Pasteurella*) *trehalosi*

have been isolated from pneumonic and healthy bighorn sheep over much of their range, although experimental work over the past half century has largely focused on *M. haemolytica* from presumptive domestic sheep reservoirs [14, 128, 173, 212, 213] (Table 3). Evidence consistent with domestic sheep Pasteurellaceae acting as a primary pathogens of bighorn includes isolation of Pasteurellaceae from pneumonic bighorn sheep during outbreaks, outbreaks in free-ranging and captive bighorn sheep following “contact” with domestic sheep and goats, pneumonia in bighorn sheep caused by experimental inoculations of isolates native to domestic sheep, *in vitro* evidence of a cellular basis for bighorn sheep’s particular sensitivity to disease from *M. haemolytica*, and experimental evidence for transmission from domestic sheep causing disease in bighorns [15, 19, 151, 214–216]. However, it has not yet been demonstrated that any Pasteurellaceae are found more often in animals with disease than in healthy animals. In addition, Pasteurellaceae of apparently healthy domestic and bighorn sheep under field conditions can be similar, and there is evidence for interspecies “contact” occurring under field conditions without disease resulting [128, 174, 217, 218]. The similarity of Pasteurellaceae among bighorn and domestic sheep may represent the historic introduction and establishment of novel strains in populations, and it is conceivable that this could predispose animals to disease. Thus, there is a need to identify Pasteurellaceae that are associated more with pneumonic bighorn sheep than with apparently healthy animals. Alternatively, it is possible that pasteurellosis is an opportunistic infection that results when favored by other host, environmental, or agent determinants. A host determinant hypothesized to favor pasteurellosis is elevated levels of corticosteroids in response to external stressors [93, 219]. There is a need to clarify the degree to which Pasteurellaceae act as primary pathogens, and whether other determinants are needed to favor respiratory disease outbreaks.

Domestic livestock, and possibly bighorn sheep, can experience a range of clinical severity to Pasteurellaceae. This includes self-resolution of infections. Histopathological evidence for resolution of bronchopneumonia suggests that bighorn sheep may experience a similar range of clinical severity and self-resolution [18, 181]. There is also evidence that pasteurellosis can cause chronic, sporadic disease that can negatively impact bighorn sheep populations, as opposed to acute outbreak impacts [41]. Isolation of bacteria such as *Arcanobacterium* (formerly *Corynebacterium* and *Actinomyces*) *pyogenes* from pneumonic bighorn sheep, and isolation of *Histophilus somni*, and other Pasteurellaceae from apparently healthy animals, are consistent with pasteurellosis as an opportunistic infection that originates from endogenous, commensal bacteria [17, 113, 153, 157, 220]. If this is true, other commensal bacteria may cause disease in the absence of Pasteurellaceae.

Strategies considered for mitigating the effects of pasteurellosis in bighorn sheep include administration of antibiotics, vaccines, and quarantine establishment. Although biomedical approaches are established and well-perceived strategies, there is a lack of demonstrated vaccine or medication efficacy to date [18, 112, 221–223]. Several explanations

are possible for this, but the dearth of published data supporting the efficacy of vaccines for pasteurellosis in domestic ruminants under field conditions illustrates the challenges of developing products and documenting efficacy [26, 224, 225]. Alternatively, 14.5 km buffers between bighorn and domestic sheep have been employed as a quarantine strategy to minimize interspecies transmission of Pasteurellaceae [226], although long-distance movements by both species can undermine this approach. Nevertheless, in principle, buffers are useful for multiple reasons, such as minimizing interspecies transmission of multiple agents, minimizing competition for forage, mitigating against potential stress responses of bighorn sheep to domestic animals, and potentially for other reasons, particularly for small-, high-risk bighorn populations. Management of environmental and host determinants may be effective alternatives to biomedical strategies [21] if validated, but delayed effects and indirect mechanisms of action may be difficult to explain for obtaining stakeholder and public support.

Mycoplasma ovipneumoniae has been considered both a primary pathogen and as a predisposing agent for secondary pasteurellosis in domestic ruminants, particularly in lambs <1 y [227, 228]. However, much as with Pasteurellaceae, *Mycoplasma* spp. appears to be a common commensal of domestic sheep, and it is believed that disease may primarily occur when favored by certain combinations of host, environmental, and agent determinants [229]. It is not clear to what extent *Mycoplasma* spp. are responsible for outbreaks in bighorn sheep (Table 3). *Mycoplasma ovipneumoniae* has been associated with bronchopneumonia in free-ranging bighorn sheep, and could be an explanation for depressed lamb recruitment in years following outbreaks [179]. However, while *Mycoplasma* spp. may be an agent that could be introduced into naïve bighorn sheep populations from domestic sheep, the percentage of free-ranging pneumonic bighorn sheep with evidence of *Mycoplasma* spp. varies from 7–55%, a bighorn sheep that closely associated for several months with domestic livestock with *Mycoplasma* spp. was apparently uninfected at necropsy, and limited experimental inoculations of bighorn sheep lambs failed to result in fatal respiratory disease [18, 19, 128, 179]. Thus, while *Mycoplasma* spp. may contribute to bighorn sheep outbreaks, multiple determinants may be required for this to occur, much as appears to be the case for Pasteurellaceae. A caveat is that *Mycoplasma* spp. is not routinely tested for, and many laboratories have a limited diagnostic capability for this agent. Therefore, our understanding of whether *Mycoplasma* spp. is partly or generally responsible for bighorn sheep outbreaks may be limited by methodology. In addition, if *Mycoplasma* is demonstrated as an important determinant of bighorn sheep respiratory disease, the limited options for efficacious treatment or vaccination of domestic livestock suggest that biomedical management options would not be available for bighorns in the near future.

Multiple bacterial species have been associated with respiratory disease in bighorn sheep, much as has been documented for other species. Outbreaks of bacterial ocular disease in bighorn sheep illustrate the potential for bacterial pathogens to be transmissible, and for livestock to be a

reservoir for transmissible bacterial pathogens [178, 180]. However, the degree to which endogenous versus transmissible bacteria generally contribute to disease is unclear, reservoirs are uncertain, factors affecting the dynamics of transmissible agents are undetermined, and the degree to which specific bacteria contribute to specific outbreaks in free-ranging populations or in general needs clarification. This uncertainty is due to constraints in methodology and study designs (predominantly case reports and cross-sectional studies) that limit the inference possible from historic data. Biomedical approaches for managing disease in domestic animals have been successful, but outside of rabies, examples of where these approaches have been effective in wildlife are limited. Furthermore, rigorously demonstrating product efficacy in bighorn sheep will require a long timeline. Based on shipping fever models of respiratory disease in livestock, development of multiple strategies for management of host and environmental determinants of bighorn sheep disease is needed for current conditions and in response to anthropogenic and climate changes.

2.4.3. Virus. Viral respiratory pathogens have been associated with bighorn sheep outbreaks, and there is serologic evidence that animals can be infected and recover from these agents (Table 3) [128, 182, 185]. This is similar to the role of viruses as primary pathogens or as agents that predispose livestock and other species to opportunistic bacterial infections [24, 208, 230]. This poses many of the same questions that exist for parasitic and bacterial infections of bighorn sheep. Method and study design limitations present challenges for determining: reservoirs for viral agents; whether viral agents act as primary respiratory pathogens; or whether other agent, host, or environmental codeterminants are required for disease to develop.

A high seroprevalence of antibodies to agents such as parainfluenza-3 and bovine respiratory syncytial virus in some bighorn sheep populations suggests that infections may be common and clinically mild or incidental [128, 184, 186]. However, the potential for disease to develop when favored by other determinants must be considered, particularly if these are nonnative agents that have become established in bighorn sheep populations. In addition, an increase in disease associated with nonrespiratory viral agents is a consideration if transmission dynamics are altered by increased population densities, climate change, or other determinants [187, 188]. Longitudinal studies of multiple populations will likely be required to determine the degree to which viruses and other determinants contribute to respiratory disease outbreaks generally or in specific instances, as well as whether disease is a density-dependent phenomena. Where viruses are primary pathogens or are a part of multiple agent infections, viral vaccines of demonstrated efficacy may decrease the prevalence and/or severity of infections, if livestock models can be applied to bighorn sheep [231].

2.5. Mixed Infections. Multiple agents have been associated with bighorn sheep outbreaks. Some reports have indicated that multiple agents were concurrently responsible for outbreaks as mixed infections, with environmental or host

determinants implicated as ultimate causes [18, 90, 113, 120]. If this is true, environmental and host determinants may need to be targeted to effectively manage outbreaks, and the specific strategies that are most effective may vary spatially and temporally. Knowledge of agents, modes of transmission, and mechanisms of disease may not be required to develop effective host and environmental management strategies for reducing respiratory disease in bighorn sheep. This perspective is illustrated by risk factor analyses that demonstrated strategies for decreasing cholera and lung cancer in humans, even though the agents and mechanisms of these diseases were not established [232, 233]. Consequently, research on risk factors for disease or indices of health may provide the most immediate information for guiding bighorn sheep management strategies.

3. Summary

Over the last century, multiple environmental, host, and agent determinants have been hypothesized as limiting for bighorn sheep populations and/or contributing to outbreaks, and a succession of agents have been investigated. If some credence is given to each report, multiple determinants may actually limit bighorn sheep populations. In addition, some determinants may have multiple effects, such as the potential for high animal densities to favor disease via competition for forage, increased “stress” responses, and increased contact for transmission of infectious agents. These determinants may be present locally or range-wide, and may be altered by climate change or anthropogenic factors. Temporal and spatial variation compounds the challenge of predicting and mitigating disease outbreaks. Furthermore, whether outbreaks are due to completely novel events, and the degree to which endemic agents and environmental conditions favor the occurrence of outbreaks, is unclear. This uncertainty creates challenges for development of management plans and has fostered contention among stakeholders with differing values and competing land use interests.

Field studies of bighorn sheep outbreaks have largely been limited to case reports and cross-sectional studies, and, therefore, have study designs with limited inference [234]. The sporadic nature of outbreaks, limited baseline data, logistic constraints, and other practical concerns present further challenges for developing rigorous study designs of outbreaks. Captive studies of bighorn sheep disease have been employed to circumvent the limitations of field work and address debate between stakeholders on the compatibility of domestic and bighorn sheep under field conditions. However, a clear, invariant relationship between a single agent and field outbreaks has not yet been documented. In part, this could be due to limitations in the available diagnostic assays and practical challenges associated with conducting field work. Therefore, many years of focusing on agents responsible for bighorn sheep respiratory disease have not yielded proven means of predicting and mitigating outbreaks. Consequently, in contrast to a reductionist approach, increased consideration of how host, agent, and environmental determinants may interact under field condition, as well as

improved characterization of “healthy” bighorn sheep populations, is needed to expedite development of practical and efficacious management strategies. A more comprehensive approach to disease in bighorn sheep is consistent with domestic animal models of managing “shipping fever” and conventional wildlife management principles [1, 23].

There has been a focus on domestic sheep as a source of infectious agents that are pathogenic to bighorn sheep [5]. This perspective is reasonable because whenever different populations mix, there is the potential for infectious agents to be transmitted from source to naïve populations. This is the basis of regulations restricting interregional movement of animals and plants [235, 236]. However, the actual degree of risk for interspecies transmission of infectious agents, the circumstances where transmission occurs, and practical strategies for minimizing interactions have not been established. In addition, a focus on agent transmission has generally taken precedence over research on competition for forage, behavioral effects, and other factors that might be relevant to interspecies interactions. Given the evidence that interspecies interactions do not invariably result in disease, currently neglected factors may be important for managing these two species in circumstances where: agricultural land is used by bighorn sheep; domestic livestock reside on private land near to bighorn sheep populations; domestic livestock are used for exotic weed control; circumstances where preservation of agricultural enterprises is important for preventing conversion of land to uses that are not compatible with the needs of wildlife; for other reasons. Thus, while protocols for minimizing interspecific transmission of infectious disease from domestic to bighorn sheep have been developed [237], there is a need for further development of practical strategies for minimizing interspecies interactions and conflict between stakeholders.

Recent die-offs of bighorn sheep in several locations suggests that the proximate cause of these events may be a shared environmental determinant. An environmental determinant could favor the development of disease from endogenous or established exotic agents. Drought could be such a determinant if it compromises host health, such as by reducing forage quantity and/or quality. The effect of precipitation quantity and timing on forage may be a useful index of animal health, due to its relationship with bighorn sheep fecundity [51, 98]. Alternatively or concurrently, if these outbreaks were due to the introduction of novel infectious primary pathogens into multiple naïve bighorn sheep populations during the same time period, effective strategies for minimizing inter- and intra-population transmission of such agents are needed. Strategies for preventing inter-specific and intraspecific transmission may not need to be agent-specific, and it may be practical to base them on existing wildlife or domestic animal management methods. In addition, prevention of agent transmission and environmental management strategies are not mutually exclusive approaches. Greater attention to host and environmental determinants of disease, as well as validation of methods for limiting epidemics, is likely to complement existing lines of research and result in multiple strategies for predicting and managing outbreaks in bighorn sheep. This is likely to result in programs that are effective in

establishing and meeting accepted population management objectives that are based on stakeholder expectations, as well as variation among local and range-wide conditions.

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