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Are We Coexisting With Carnivores in the American West?

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Human-carnivore coexistence is an oft-stated goal but assumptions about what constitutes coexistence can lead to goal misalignment and undermine policy and program efficacy. Questions about how to define coexistence remain and specific goals and methods for reaching coexistence require refining. Co-adaptation, where humans adapt to carnivores and vice versa, is a novel socioecological framework for operationalizing coexistence but has yet to be comprehensively examined. We explored co-adaptation and two additional coexistence criteria through analysis of three case studies involving large carnivores in the American West, each addressing differing approaches on how and what it means to coexist with carnivores: Mexican gray wolves (*Canis lupus baileyi*) in Arizona and New Mexico, grizzly bears (*Ursus arctos horribilis*) in the Greater Yellowstone Ecosystem and coyotes (*Canis latrans*) throughout the American West. We used a multiple case study design that analyzed within and across cases to understand coexistence broadly. For each case, we asked (1) are landscapes shared in space and/or time, (2) is co-adaptation occurring and (3) do stakeholders consider risks tolerable? To identify whether coexistence criteria are met, we investigated peer-reviewed published articles and news media and conducted key informant interviews. We found clear evidence to support land-sharing between humans and coyotes and limited spatial overlap between humans and grizzly bears and Mexican gray wolves. Co-adaptation was variable for wolves, possible with bears and clearly evident with coyotes. Tolerable risk levels are likely achievable for bears and coyotes based on the available literature assessing risk perceptions and tolerance. But disagreement regarding risk management is a driver of conflict over wolves and persistent barrier to achieving coexistence among diverse stakeholders. Patterns in coexistence criteria did not emerge based on taxonomy or geography but may be influenced by body size and behavioral plasticity. The common key to coexistence with each considered carnivore may be in more equitable distribution of costs and benefits among highly diverse stakeholders. Better understanding of these three coexistence criteria and innovative tools to achieve them will improve coexistence capacity with controversial carnivores on public and private lands in diverse American West contexts and beyond.

Keywords: Mexican gray wolves, coyotes, grizzly bears, co-adaptation, risk perceptions

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INTRODUCTION

Human-wildlife coexistence is an oft-stated goal but implicit assumptions about what constitutes coexistence can lead to goal misalignment and undermine policy and program efficacy (Fischer et al., 2014). For example, some conservationists envision coexistence as land sharing with wildlife (i.e., humans and wildlife occupying the same areas; Johansson et al., 2016; Crespin and Simonetti, 2019). Others consider land sparing (e.g., conserving wildlife in protected areas and discouraging them from human-dominated landscapes) a more realistic version of human-wildlife coexistence (Vucetich and Macdonald, 2017). Differing viewpoints on whether and how humans can share landscapes with large carnivores is particularly contentious given the perceived risks associated with carnivores and can influence or impede conservation actions (Lute et al., 2016; Bruskotter et al., 2017). For example, electrified fencing to spatially separate wildlife from human-occupied areas would be considered an appropriate conservation action from advocates of land-sparing but not for land-sharing. Although diverse perspectives and debate are important for progressing policy, conflicting goals and a lack of agreement regarding how and where to conserve carnivores may divert or waste limited resources. Thus, questions about how to define coexistence remain and require answers while specific goals and methods for reaching coexistence still need refining.

Challenges to coexistence come in diverse forms depending on the carnivore species and local context, which includes stakeholders near and far (because non-locals may still have an interest or stake in the existence and conservation of a species), culture, landscape, history, ecology and essentially everything encompassed in a socioecological system (Carter et al., 2014, 2017; McGinnis and Ostrom, 2014; De Vente et al., 2016). Coexisting with a habitat specialist like a wolverine (*Gulo gulo*) will be expressed in different ways, and may be easier, than coexistence with a generalist like a coyote who is more likely to range near human-dominated environments (Gehrt et al., 2009). Wolverines do not typically eat the animals that humans value in North America (in contrast to human-wolverine interactions in Europe; Persson et al., 2009). In addition, they live in remote mountain habitats that humans are less able to exploit and generally encounter humans at low frequencies. Thus, coexistence with wolverines requires fewer concessions by humans (climate change aside) compared to omnipresent coyotes or suburban cougars (*Puma concolor*) that, although infrequent, may predate on free-ranging companion animals or livestock. In such cases, coexistence might require perceptual shifts among human communities to be more tolerant of carnivores' presence and activities as well as changes in human behavior to prevent depredation or discourage carnivore activity in certain places.

Carter and Linnell (2016; p575) define coexistence as a "dynamic but sustainable state in which humans and wildlife co-adapt to living in shared landscapes where human interactions with wildlife are governed by effective institutions that ensure long-term wildlife population persistence, social legitimacy, and tolerable levels of risk." Recent research confirmed that the key elements of this definition are supported by a global community of conservation professionals: broad consensus was found for (1) shared landscapes, (2) co-adaptation (with highest agreement with human adaptation to carnivores) and (3) tolerable levels of risk (i.e., human acceptance of some conflict) as requirements for human-carnivore coexistence (Lute et al., 2018). Although scholars have debated and refined differences in defining tolerance and acceptance (as well as stewardship), we use them synonymously here because our purposes are to understand attitudes and behaviors that influence coexistence broadly (rather than focus on the relative nuances of particular attitudes and perceptions; Treves and Martin, 2010; Bruskotter and Fulton, 2011; Treves, 2012).

Much of the scholarship exploring and defining coexistence has been conceptual or has addressed coexistence implicitly without definition (Gilroy et al., 2014; Lopez-Bao et al., 2015; Carter and Linnell, 2016; Bergstrom, 2017; Linnell and Kaltenborn, 2019). Rigorous assessment is needed to understand how these theoretical concepts operationalize in specific cases. With Carter and Linnell's (2016) definition of coexistence as a foundation, we attempted to root abstract ideals of coexistence in real cases by qualitatively exploring whether coexistence is being achieved—or at least implicitly or explicitly a goal of carnivore conservation—in three case studies in the American West: coyotes (*Canis latrans*) throughout the western US; grizzly bears (*Ursus arctos horribilis*) in the Northern Rockies; and Mexican gray wolves (*Canis lupus baileyi*) in the southwestern US (**Figure 1**). We use the term carnivore for mammalian species in the order Carnivora and, in these cases, who eat other animals and encounter conflict with humans because of it, while recognizing that coyotes and grizzly bears are omnivores with varied reliance on animal protein (Wolf et al., 2018). We focus on the American West because the region consists of a mosaic of land-cover types, with large amounts of public land under varying degrees of protection, use, and ownership. This public land supports high levels of connectivity and habitat for wildlife populations, including those with large resource requirements such as large and wide-ranging mammals (Barnes et al., 2016; Expósito-Granados et al., 2019). However, these wildlife populations are under threat from energy development projects, urban and ex-urban sprawl, increasing road traffic and density, and amenity-driven human migration (Leu et al., 2008). In response to these shifts, the American West is experiencing shifting cultural norms and values related to biodiversity conservation and natural resource management that create new challenges and opportunities for coexisting with carnivores (Dietsch et al., 2019). These shifts may signal what other regions (e.g., Brazilian grazing systems) might expect and may provide a useful test bed for the kinds of policies and institutions needed to foster coexistence elsewhere (Jones et al., 2019). The local insights gained from exploration of the main coexistence criteria in these case studies will therefore help understanding and operationalizing the global challenge of

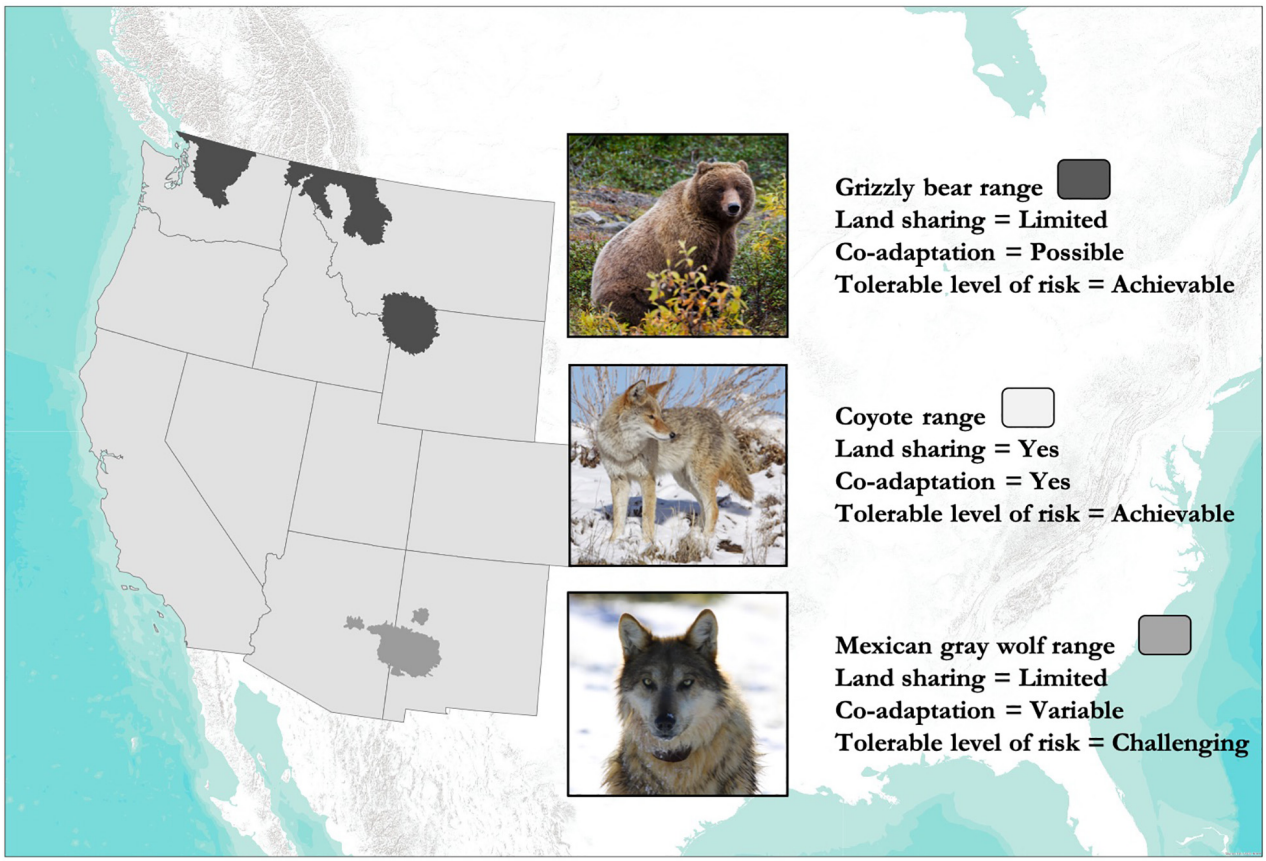

FIGURE 1 | Map of the American West and case study species. Within the conterminous United States, grizzly bears currently range in Idaho, Montana, Washington, and Wyoming. Their geographic range extends into Canada but is not shown here. Mexican gray wolves are currently in Arizona and New Mexico, as well as Mexico (not shown). Coyotes range across the 11 western United States and beyond. Mexican gray wolf photo courtesy of United States Fish and Wildlife Service. Grizzly bear and coyote photos from member skeeze on Pixabay.com. Range data from: United States Geological Survey – Gap Analysis Project, 2018, United States Geological Survey – Gap Analysis Project Species Range Maps CONUS_2001: United States Geological Survey data release, https://doi.org/10.5066/F7Q81B3R.

coexistence by revealing patterns without losing sight of rich, contextual knowledge.

METHODS

We used qualitative inquiry to allow open-ended exploration of the three criteria, which are not yet well-defined in the literature (see details below), as well as any other relevant themes that emerge from literature review or key informant interviews. Exploratory qualitative inquiry is appropriate for this study's objectives because it does not constrain data to researcher-defined ideas (Ivankova et al., 2006). To qualitatively assess three key elements of human-carnivore coexistence in the American West, we selected three case studies that: (1) were geographically representative of diverse carnivore species in the American West, (2) addressed differing approaches and perspectives on how and what it means to coexist with carnivores (e.g., because each species presents unique challenges based on life history differences), (3) provided an opportunity to reveal ways in which to resolve an existing and evolving problem (e.g., by exploring the unique factors involved in and ongoing conservation challenges of each case), and (4) had sufficient information available (e.g., triangulated data from multiple information sources, interviews). Of course, it would be useful and valid to include any other large carnivore species that interact with humans and present challenges to coexistence. We chose to focus on species with immediate need to improve coexistence based on the extent to which these species are imperiled, vilified and exploited (Wayne and Hedrick, 2011; Marshall et al., 2016).

We used a multiple case study design that analyzed within and across cases (Ivankova et al., 2006). For each of the three case studies, based on the definition of coexistence in Carter and Linnell (2016), we asked (1) are landscapes shared, (2) is co-adaptation occurring in ways that promote coexistence and (3) do stakeholders consider risks tolerable? We manually searched in Web of Science and Google Scholar and analyzed peer reviewed published articles, theses and traditional news media. Search terms used included: "coexistence" and "co-existence," "perceived risk," "tolerance," "acceptance," "cultural carrying capacity," "social carrying capacity," "human-[species] conflict," "human-carnivore conflict," "adaptation," and "co-adaptation"

with boolean expressions to link these phrases with each case study (e.g., " 'perceived risk' AND 'grizzly bear' "). Iterative searches occurred through three avenues. (1) We first searched databases (e.g., articles from the above search engines would sometimes link to other databases, such as Science Direct), which would then suggest additional relevant studies. (2) We reviewed literature cited sections of particularly relevant studies based on title and then abstract to discover additional studies for review. (3) We then gathered key informant suggested studies (further described below). To screen these additional studies, titles were assessed for keywords (i.e., those used in the first round of literature search). If a study passed title screening, we read the abstract to confirm the study's relevancy to one of the three case studies (CEE Guidelines 2013). All reviewed abstracts were deemed relevant enough for full review and applied to one of the three case studies. Studies that did not provide information regarding the three questions (e.g., did not address spatial overlap or lack thereof, adaptation between humans and carnivores, risk perceptions) were not necessarily included in the results and literature cited. Given the qualitative and exploratory nature of this analysis, we did not aim for saturation or full representation of the case studies. Literature review was considered complete when enough information was gathered to either (a) answer the three questions or (b) provide evidence that insufficient research has been conducted to answer the three questions for each of the three case studies.

Key informants were included in this qualitative case study analysis as external validation and triangulation of other information sources (e.g., the authors prior expertise and knowledge of these cases, peer-reviewed studies, media coverage) and to support, validate and add studies to the literature review process (Lynam et al., 2007). Key informants are non-randomly selected interviewees chosen for the their breadth and depth of knowledge on the case study (Lavrakas, 2008). We identified informants based on their leadership in the conservation of each species (e.g., led or played an integral role in recovery efforts, advocacy, policy reform), interviewed one key informant per case study (see **Supplementary Material** for semi-structured interview guide). Key informants were scientists currently or formerly working in various institutions (e.g., governmental and non-governmental organizations) with at least two decades of experience in the case study species. We asked key informants to suggest any studies known to be germane to the case study in question. Suggested studies were subjected to the screening process outlined above.

In our exploration of the three criteria for coexistence, we found that definitions and interpretations of those criteria varied among scholars. Land sharing can be said to occur if carnivores and humans overlap spatially, but not necessarily temporally (Carter et al., 2012, 2013). Spatial overlap and whether it denotes coexistence is debated in the literature (Carter et al., 2012, 2013). For example, one researcher may describe spatial overlap as any co-occurrence of a carnivore and human or human activity; others might argue that a certain degree of overlap is required (e.g., consistent use and occupation of the same space by both species over a certain timeframe) to claim land sharing. We deferred to the literature and key informants as to whether spatial overlap was considered to be occurring by any of these measures.

Co-adaptation is also difficult to assess given the context-dependency and need for more research. For our purposes, adaptation is defined not in the evolutionary sense but in the sense of individuals pursuing their own interests by learning and responding to the other species' behavior (Carter and Linnell, 2016). When such adaptations are not at the expense of the other species, then we characterize them as being conducive to coexistence, which is the focus here. For example, a carnivore's learned response to human presence or various behaviors may enhance that animal's fitness (e.g., better forage opportunities) while leaving unchanged the risk or costs of those animals to humans. Human adaptation to carnivores may come in the form of non-lethal methods and other preventative measures that avoid conflict.

Finally, identifying if and under what circumstances tolerable levels of risk exist requires tailored social science of diverse stakeholder groups and/or in depth observation that comes from working in participatory conservation. Tolerable levels of risk vary greatly among different stakeholders depending on experience, knowledge of the carnivore species, sociodemographic characteristics, and various moral positions, worldviews and values (Kellert, 1985; Carpenter et al., 2000; Lute et al., 2016). No single definition of tolerable risk exists. For the purposes of this manuscript, we refer to tolerable risk as a level of potential conflict between humans and large carnivores that results in human acceptance of the presence of large carnivores and little evidence that human retaliation to that conflict will seriously jeopardize the species or individual carnivores living near humans. Where specific social science measuring risk perceptions of diverse stakeholders was lacking, we relied on information from key informants.

RESULTS

Coyotes Throughout the American West

Are Landscapes Shared?

Of all the case studies, coyotes present the clearest example of land sharing between people and the carnivore in question. Coyotes are now found in every habitat from Yellowstone National Park to Chicago's O'Hare International Airport, having expanded their original Southwestern range to include most of the contiguous United States (Gehrt et al., 2010). Their ability to survive high degrees of spatial overlap with humans may be in part due to their ability to use natural cover to avoid detection (Poessel et al., 2017).

Is Co-adaptation Occurring?

Coyotes' ability to avoid the humans they live close to is an indication of their contribution to our second consideration for coexistence: co-adaptation. Coyotes adapt to humans with behavioral plasticity that allows them to compensate anthropogenic mortality with higher fecundity (Knowlton et al., 1999). One might argue this plasticity is not an adaptive response directly to humans but simply the nature of coyote life history.

Regardless, coyotes demonstrate a clear ability to adapt to human activity and exploitation (Gehrt, 2007; Gehrt et al., 2009; Gehrt and Brown, 2011).

But co-adaptation is a two-way response. Do humans adapt to coyotes? At least in a few places, the answer is yes. Urban coyote projects with goals to track and protect coyotes exist across North America from Portland, Oregon to New York, New York[1]. One clear example of community-driven coexistence, Marin County, California replaced lethal control with a non-lethal program where cost-sharing funds tools such as fences and guard dogs to protect sheep from coyotes (Fox and Papouchis, 2005; Fox, 2006). Given the ubiquitous presence of coyotes across the continent, residents likely are actively adapting to the presence of coyotes (e.g., by removing tempting food sources, observing coyotes from a distance) in many suburban, urban and perhaps even rural areas, but these actions do not necessarily make the news and are difficult to quantify without further research. One key informant supported this idea, that the "vast majority of residents are silently coexisting" with coyotes but also suggested that a vocal minority of urban residents perceive coyotes to be dangerous and needing relocation. Relocation may be the urban manifestation of "not in my backyard" intolerance, with its rural equivalent being more lethal actions.

Do Stakeholders Consider Risks Tolerable?

Similar to urban-rural differences in limits to human willingness to adapt to coyotes, what is considered a tolerable level of coyote-related risk may vary over time and based on local context. Over 30 years ago, a national level survey of public attitudes about coyotes found them among the least liked animals (Kellert, 1985). Increasingly recent research has found improved perceptions toward coyotes (Stevens et al., 1994; Vaske and Needham, 2007; Jackman and Rutberg, 2015). Jackman and Rutberg (2015) found that mean acceptance of coyotes shifted from negative to positive (in a scale of −2 to +2, −0.28 in 2005 to 0.19 in 2012) and support for eradication of coyotes dropped from 18% in 2005 to 6% in 2012. They also reported decreases in mean acceptance of lethal coyote control from 2005 to 2012 (0.01 to −0.31 in a −2 to +2 scale). Vaske and Needham (2007) report similar findings with majorities finding lethal coyote control unacceptable (23%) or only acceptable if they injured or killed pets (42%). But negative attitudes exist, especially in areas with media coverage of negative human–coyote interactions (Sponarski et al., 2015a, 2016; Frank et al., 2016). Research has revealed varying levels of risk perception among residents who had observed coyotes from a newly established population (lower fear reported in Elliot et al., 2016; higher in Lu et al., 2016). Even within a single state, different cultural identities may result in varying risk perceptions related to coyotes (Drake et al., 2020). Generally, one could conclude that public attitudes toward coyotes is equivocal (Sponarski et al., 2015b; Elliot et al., 2016).

One key informant observed that the longer coyotes are present, the higher the tolerable level of risk, which is supported by research on coyotes and other carnivore species (Wieczorek Hudenko et al., 2008). People perceive novel risk as much more threatening than familiar risks, whether the source of perceived risk is a coyote or a new technology (Slovic, 1987). Differences in risk perception, as well as worldview, personality, experience and other attitudinal influences (the subject of much human dimensions research, e.g., Kellert, 1980; Fulton et al., 1996; Dressel et al., 2015), may explain why certain ranchers accept carnivore-related risk to their operations. As coyotes establish new territories across the American West, and beyond, acceptance of some risk may shift depending on whether people adapt to coyotes by preventing conflict. Without conflict prevention, potential conflict is allowed to continue and associated actual and perceived levels of risk will likely be higher than if conflict is effectively prevented. Alternatively, if people learn how to adapt to coyotes (Sponarski et al., 2016) and, as one key informant highlighted, to read coyote behavior to differentiate positive or neutral versus negative interactions, perceived levels of risk may reach acceptable levels and coexistence can be achieved.

Are We Coexisting With Coyotes?

Given that the majority of coyotes live near humans without major incident, coexistence with coyotes seems to be occurring among most stakeholders in diverse locations from agricultural and suburban Marin County, California to urban Los Angeles, California where residents are unaware or habituated to the presence of coyotes (Fox, 2008; Elliot et al., 2016). Conflict is relatively rare and occurs where coyotes utilize anthropogenic food sources (Gehrt et al., 2009; Poessel et al., 2017).

But exceptions to the broader coexistence pattern exist. Coexistence is likely not yet achieved in places where tolerance is low for the presence of coyotes, such as communities in Western states that organize coyote killing contests where participants are encouraged to kill coyotes with cash and other prizes (Bixby, 2015; see also Nie et al., 2017). Large scale exploitation such as killing contests is unlikely to reduce conflict and may exacerbate conflict in some situations (Treves et al., 2016; Eklund et al., 2017). Furthermore, coyotes are managed in most states as pests or game species with few restrictions. Federal programs like the United States Department of Agriculture's Wildlife Services under the Animal and Plant Health Inspection Service dedicate vast resources to killing coyotes (Bergstrom et al., 2013). In 2016, Wildlife Services used a variety of lethal tools, including aircraft, traps and poisons, to kill 76,963 coyotes and destroy 430 dens (without counting young of year that are killed during den destruction; USDA-APHIS 2017). These efforts are typically focused on reducing coyote depredation during lambing seasons but are increasingly under scrutiny for being ineffective due to coyotes' capacity for compensatory breeding (Crabtree and Sheldon, 1999). Given that wide-spread eradication efforts are the opposite of any logical definition of coexistence, we can safely say coexistence with coyotes is quite varied across urban-rural gradients of the American West.

Grizzly Bears in the Northern Rockies

Are Landscapes Shared?

Unlike coyotes but like many large carnivores that have been historically exploited by humans, grizzly bear density is

[1]https://urbancoyoteinitiative.com/collaborate/

roughly inverse to that of human population density (although empirically validated links are complex; Mattson and Merrill, 2002; Mowat et al., 2013). A long history of humans and grizzly bears sharing landscapes exists in North America and likely fluctuated with bear food availability (Mattson and Merrill, 2002). Although humans may have limited bear distribution on the Great Plains (Mattson, 1998), relatively peaceful spatial overlap occurred in California over long time frames in the past (Storer and Tevis, 1955). Currently, grizzly bears in the contiguous United States exist only in five small, isolated populations in the Northern Rockies (northern Continental Divide, Yellowstone, Cabinet-Yaak, Selkirk, and North Cascades regions). The Yellowstone population is almost completely located within a national park. The other populations are in areas of low human density, such as the Cabinet-Yaak. Yet grizzly bears and humans interact in certain habitats that are attractive to both species (e.g., a combination of human recreational areas, dispersed residences or ranching operations and bear food sources like the Flathead Valley of western Montana), sometimes resulting in conflict and bear mortality (Lamb et al., 2017). If one counts domestic cows that graze in grizzly habitat, spatial overlap can be said to occur in several areas of western Montana and northern Idaho. But again, like many large carnivores, the majority of grizzly bears die from hunting and non-hunting anthropogenic mortality (e.g., from state wildlife agencies, poachers, train and vehicle collisions; Mattson and Merrill, 2002; Mowat and Lamb, 2016). Thus, land sharing between grizzly bears and humans is occurring in some areas, especially those with low human densities, and is currently limited primarily by human intolerance, habitat loss and modification, and climate change impacts to important food sources (Doak and Cutler, 2014; Bruskotter et al., 2016; Cristescu et al., 2016; Coops et al., 2018).

Is Co-adaptation Occurring?

Evidence for human-grizzly co-adaptation exists but is limited. Grizzly bears adapting to use human food sources is well documented (Kavčič et al., 2015; Lamb et al., 2017). As omnivores, bears are adaptable to human-modified landscapes, which also means human–bear interactions are more varied (Morehouse and Boyce, 2017). Grizzlies may be learning (or forced) to avoid humans spatially (Coleman et al., 2013) and some studies suggest a link between roads or developments and lower bear density at fine spatial scales (Ciarniello et al., 2007; Nellemann et al., 2007). On the other hand, female and subadult male bears can disproportionately occur closer to human settlements due to habituation to humans and food conditioning as well as to avoid adult males (Elfstrom et al., 2012; Cristescu et al., 2016). Elfstrom et al. (2012) argue this use of human settlements as predation refuges is adaptive in avoiding aggressive male bears. But close proximity to humans can be maladaptive if human responses are conflictual and where increased anthropogenic risk occurs (e.g., vehicle and train collisions). Ecological traps, in the form of particularly attractive habitats (e.g., those dense with huckleberries) with high potential for interactions, including conflict, with humans but few evolutionary cues, suggest that grizzly bears have little capacity to assess costs of human interactions versus benefits of high-density and -quality food resources (Lamb et al., 2017).

Modern human adaptation to bears is most clearly evidenced among stakeholders using non-lethal methods of preventing conflict (e.g., monitoring cattle). The prevalence of these adaptive human behaviors varies by landscape. Areas of intense livestock grazing, where bears that are considered a "problem" or "nuisance" are killed, present the lowest prevalence of human adaptation. Yellowstone and Glacier National Parks present perhaps the highest prevalence of adaptation with park authorities incentivizing and enforcing preventative measures (e.g., carrying bear spray when hiking, maintaining safe distances) and visitors complying as well as investing time, money and other resources toward appreciation of bears and other park wildlife. Adaptation to grizzly bears outside of protected areas include shifting tolerance toward the presence of bears and removal of attractants (e.g., unsecured garbage, pet food, and livestock carcasses). Adapting to the increasing presence of grizzlies in Montana, a group of ranchers partnered with government agencies and non-government organizations to identify and implement methods for preventing conflicts, such as shifting from barb wire to electric fencing around calving pastures or composting livestock carcasses at centralized drop-off locations instead of on the private ranches (Wilson et al., 2014). Economic measures, such as subsidy programs that incentivize non-lethal methods, might also be considered adaptive (Karlsson and Sjostrom, 2011).

Do Stakeholders Consider Risks Tolerable?

To the extent that intentional anthropogenic mortality is a major limitation to grizzly distribution, it would also appear that human tolerance of grizzlies is limited, at least among some residents in grizzly bear range. A dearth of social science on attitudes related to grizzly bears in the American West makes quantifiable answers to this question challenging. The few studies that explore public perceptions of brown bears in various geographies suggest general support for their conservation, concern for risks *to* bears rather than *from* bears and that conflict is rooted in issues of governance and land-use conflict more than direct human–bear interactions (Decker et al., 2006; Clark and Slocombe, 2011; Richie et al., 2012; Parker and Feldpausch-Parker, 2013; Bruskotter et al., 2016; Heeren et al., 2017; Karns et al., 2018). Kellert's (1994) summary of research from the 1980s and 1990s suggests broad support for grizzly bears and willingness to adapt to them (Jope and Shelby, 1984; McCool and Braithwaite, 1989). Humans often view species considered rare or endangered more favorably (Kellert, 1980; Tisdell et al., 2005; Lute and Attari, 2016); therefore perceptions measured decades ago when grizzly bears were even more rare than today should only be cautiously extrapolated to current conditions. Tolerance will depend on individuals' perceptions of risk and whether conflict has been experienced (Decker et al., 2006).

In areas where local residents and ranchers currently live with grizzly bears and policy discourse is not highly conflictual, levels of risk are likely tolerable. More recent qualitative studies in contexts outside the American West suggest that fear of brown bears is relatively limited to threats to ranching and

industrial development (Hughes, 2018; Hughes and Nielsen, 2019). Exurbanites and other publics living with bears show some fear of grizzly bears but generally support their conservation, bans on hunting them and participation in non-lethal conflict and damage prevention (Hughes and Nielsen, 2019; Leveridge, 2019). Notable examples include tolerant ranchers like the B Bar Ranch in the Tom Miner Basin or operators participating in the Blackfoot Challenge in the Blackfoot River Valley[2,3]. Importantly, even where tolerance is common among residents, as one key informant pointed out, "it doesn't take many bad apples to spoil the batch. some intolerant folks breed conflicts given how widely bears range and how indelible food experiences are."

Are We Coexisting With Grizzly Bears?

Evidence exists for cautious optimism that coexistence is currently occurring because people (and their domestic livestock) are sharing landscapes with bears; humans are adapting to bears through non-lethal methods of preventing conflict; bears are apparently adapting to the presence of humans; and at least some ranchers accept some level of risk by allowing some depredations to occur without retaliation. Coexistence in this context is tenuous due to future environmental change from climate impacts on food sources and availability, human development in grizzly bear habitat and the possible interaction of these changing dynamics (e.g., reduced natural food availability may encourage shifts to anthropogenic food sources from cow carcasses to compost; Coops et al., 2018; Laufenberg et al., 2018). Regulatory changes to grizzly bear protections may also shift current human–bear dynamics in ways that are difficult to predict. Removal of Endangered Species Act (ESA) protections will likely result in one or more state-sponsored recreational hunts (as was observed in the attempted de-listing of grizzly bears in the Yellowstone distinct population segment; US National Park Service, 2019). One key informant predicted that delisting would accommodate behaviors (e.g., recreational hunting) that would not advance coexistence.

Mexican Gray Wolves in Arizona and New Mexico

Are Landscapes Shared?

As habitat generalists, gray wolves can and do live in close proximity to humans and human activity across their shared ranges. Mexican gray wolves, a distinct subspecies of gray wolves, were greatly reduced in number through eradication campaigns that reached their zenith in the 19th century and first half of the 20th century (Musiani and Paquet, 2004; Leonard et al., 2005; Wayne and Hedrick, 2011). Negative perceptions and fear of wolves, coupled with strong intolerance among agricultural and ranching communities, motivated the campaigns to eradicate wolves through bounty systems and with diverse lethal tools. Although these perceptions remain to some degree among contemporary stakeholders (particularly in rural and agricultural-reliant communities), much of the fear over wolves has subsided in the general public and other stakeholders, allowing wolves to be actively reintroduced or passively tolerated in their recolonization of past territories (Smallidge et al., 2008; Ashcroft et al., 2010).

In the case of Mexican gray wolves specifically, opportunities for spatial overlap are possible but severely reduced and not currently occurring in large part because state agency decisions focus wolf recovery efforts on remote and public lands in Arizona and New Mexico. While not entirely focused on protected areas, a large amount of the current Mexican wolf experimental population area (MWEPA) is focused on National Forest lands where conflict is expected to be minimal. As one key informant explained, recovery goals are "limited both in abundance and geographic distribution, such that humans will determine how many wolves will exist and where." While this informant acknowledged the states' "fair honest intent" to recover wolves in the MWEPA, their efforts have "stopped prematurely and short of recovery" in a manner "not in spirit and intent of the ESA." Despite evidence from other contexts and increasing knowledge and efficacy of non-lethal methods, shared landscapes among Mexican gray wolves and humans are currently limited deliberately by humans.

Is Co-adaptation Occurring?

Evidence for human-wolf co-adaptation is variable. The evidence for wolves' adaptive response to humans include learned behavior to avoid traps (lethal and non-lethal), snares and poisons (Young and Goldman, 1944; Treves and Karanth, 2003; Smallidge et al., 2008) while taking advantage of roads to ease movement, especially in winter (Muhly et al., 2019). Wolves also have, perhaps in the long-term maladaptively, learned to replace declining native prey with domestic species such as cows and sheep. Humans in turn have adapted to wolf depredations with varying non-lethal tools, including fences, fladry, noise and light-based deterrents, and guardians [both human (e.g., shepherds and range riders) and non-human (e.g., dogs, llamas, and donkeys)]. As the best available science continues to measure and improve non-lethal methods, the potential for humans to adapt to wolves is great (Treves et al., 2016; Bergstrom, 2017; Stone et al., 2017).

While reintroduced wolves have learned to effectively hunt native and non-native prey on their own (a sort of adaptation or resilience to human interference), the population still requires human support via genetic rescue (e.g., injections of new genes through captive-rearing and cross-fostering of pups). The continued need for genetic rescue of the Mexican gray wolf population may be due less to a lack of wolf adaptive capacity but more to anthropogenic mortality and mis-management (i.e., delayed and limited releases of new captive-reared individuals; Hedrick and Fredrickson, 2010). Thus, although currently limited by human motivation and management, the potential for co-adaptation is not only possible but promising.

Do Stakeholders Consider Risks Tolerable?

The high level of risk perceptions among some wolf stakeholders may be the greatest challenge to human motivation and management to share spaces and adapt to wolves. Although

[2]www.bbar.com

[3]blackfootchallenge.org

few dedicated studies have focused on risk perceptions related specifically to Mexican gray wolves, much research has been conducted on human perceptions related to fear of and tolerance for gray wolves in similar contexts of the American West (e.g., Houston et al., 2010; Bruskotter et al., 2014; Slagle et al., 2017). These studies suggest that significant barriers to wolf conservation exist in the correlated relationships between low tolerance, high risk perceptions and support for lethal control of wolves among some rural stakeholders that share spaces with wolves (Linnell et al., 2003; Lute and Gore, 2014a; Mech, 2017; Lute and Gore, 2019). Among other public stakeholders though, tolerance is generally high and relatedly, support for wolf-related stewardship and conservation is high (Bruskotter and Wilson, 2014; Lute and Gore, 2014b; Lute et al., 2016). This tolerance gap among stakeholders makes finding a single level of acceptable risk difficult. Risks posed by wolves to human interests, while low, will likely never be completely eliminated and thus this element of coexistence will not be achieved until risk perceptions shift among key stakeholders.

Are We Coexisting With Mexican Gray Wolves?

Disagreement regarding risk is a driver of conflict over wolves and a persistent barrier to achieving coexistence among diverse stakeholders. Yet, given the high degree of potential spatial overlap and co-adaptation, coexistence is very possible if the potential risks posed by wolves can be mitigated and prevented with equitable and transparent policies and practices. Until then, increases to the current population level—around 131 Mexican gray wolves—may remain stymied by anthropogenic mortality (US Fish and Wildlife Service, 2017a,b).

ANALYSIS ACROSS CASE STUDIES AND DISCUSSION

Our analysis of case studies did not reveal clear patterns based on carnivore taxonomy (i.e., *Canis* spp. vs. *Ursus* spp.) or geography. We found evidence to support land-sharing between humans and coyotes and limited spatial overlap with grizzly bears and Mexican gray wolves. Co-adaptation was variable for wolves, possible with bears and clearly evident in the case of coyotes. Tolerable levels of risk are likely achievable for bears and coyotes based on human dimensions studies assessing risk perceptions and tolerance. Overall, the strongest evidence exists for human-coyote coexistence, followed by coexistence with grizzly bears. Given the contentious nature of Mexican gray wolf management among oppositional stakeholders, coexistence in this realm likely requires more and better conflict resolution between human groups (Redpath et al., 2015; Lute and Gore, 2019).

Coyotes' smaller body size and behavioral plasticity may be allowing greater coexistence capacities vis-à-vis all three coexistence criteria. Larger-bodied wolves and grizzly bears may challenge humans' tolerance of actual and perceived risks. But disagreement over wolf-related risks, perhaps more so than bears, is a persistent barrier to achieving coexistence. Preliminary research suggests that human fear of wolves is more rooted in mistrust of institutions compared to fear of bears (Johansson and Karlsson, 2011; Johansson et al., 2012). Although public discourse includes fearful rhetoric about wolves' predatory behavior toward humans (Barnes, 2013; Berlin, 2013; a legitimate concern more so in contexts outside North America, e.g., Behdarvand et al., 2014), measured risk perceptions of wolves have been associated with vulnerable others (e.g., domestic animals) over personal safety and interests (Lute and Gore, 2019). Thus, although bears attack humans more than wolves do (Penteriani et al., 2016), risk associated with wolves seems to dominate policy discourse (Chandelier et al., 2018; Killion et al., 2018) and impede the pursuit of a shared and acceptable level of risk. This discrepancy may be rooted in biases that arise from human perceptions of species and their traits (Lorimer, 2007; Veríssimo et al., 2017). Fear of wolves may be heightened by the intimidating image of wolves cooperative hunting, whereas people see human-like characteristics in bears (Flykt et al., 2013).

The politics of the ESA in the American West may also be driving coexistence differences reviewed herein. Unlike wolves and grizzly bears, coyotes have not been listed as endangered or threatened. In contrast to the claim that endangered species status has resulted in a particularly high level of animosity toward endangered carnivores such as wolves from rural stakeholders (for review and counterpoint see Bruskotter et al., 2018), the loci of control for coyote management has always been in the hands of local people. Local, decentralized control over management of coyotes may explain why we observe both promising coexistence capacities as well as significant eradication efforts in all western states (and most states where they range; Fox and Papouchis, 2005; Bergstrom et al., 2013). Furthermore, politization of wolf conservation may simply be a step ahead of bear conservation. If grizzly bear recovery continues and leads to ESA de-listing, the predator pendulum swings in policy observed with wolves may occur with bears as well.

Patterns among and between carnivore coexistence cases require more exploration. For instance, various combinations of carnivore species characteristics such as body size, omnivory, habitat generalism, behavioral plasticity or other traits on which human perception may focus (e.g., rarity, familiarity, intelligence, human-like traits, aesthetical values, and ecosystem services) may influence likelihood of coexistence (Lute and Attari, 2016). Likewise, quantifying and comparing tolerable levels of risk across different stakeholder groups remains an important, yet challenging, area of future work. Future research along these lines might focus on improving or incorporating tools from other disciplines to measure and identify where tolerable risk exists among divergent stakeholders. New frameworks that facilitate evaluation of the tradeoffs in the ecosystem services and disservices (i.e., risks and costs) of carnivores in shared landscapes is a promising way forward by incorporating diverse wildlife perspectives within hierarchical social and governance contexts (Ceauşu et al., 2019). Additional research

is needed to quantify these hypotheses and advance discussion beyond speculation.

CONCLUSION AND MANAGEMENT IMPLICATIONS

Given the polarity of human perceptions about carnivores, coexistence—defined by land sharing, co-adaptation and tolerable levels of risk—with carnivores in the American West is only occurring in certain contexts. Coexistence in a human-dominated world likely will not occur where only one of the three focal elements exists, but instead when there is a combination of the three elements. Importantly, additional factors beyond the scope of this paper, such as effective institutions and their social legitimacy, will also likely be keys to coexistence (Carter and Linnell, 2016). The limits of our current capacity for coexistence reside in challenges related to risk perceptions and spatial overlap. Risk could be rendered irrelevant with a high degree of land-sparing, where large swaths of public lands were protected with spatial zoning for coexistence that would necessitate land-use planning to accommodate ecological corridors, refugia, and core habitats (Linnell et al., 2005). Otherwise, perceived and acceptable levels of risk must match for coexistence to occur where humans and carnivores share landscapes.

Currently, coexistence is limited by asymmetry of risks and resources related to living with carnivores (Carter et al., 2019). It is a long-held belief that human-wildlife conflict (i.e., direct antagonistic interactions between humans and wild animals) is a result of rural residents and ranchers incurring many of the direct costs (e.g., livestock depredation), receiving few benefits and resenting a situation that feels forced by the federal government and urban elites (Wilson, 1997; Nie, 2001). In this context, resources are often considered in financial terms and rural residents and ranchers are assumed not to have the resources to cope with or prevent depredation (hence, conflict responses include compensation programs and subsidized fencing; Berger, 2006; Dickman et al., 2011; Karlsson and Sjostrom, 2011; Packer et al., 2013). Household income has also been shown to influence attitudes, allowing urban stakeholders—or affluent "hobby" ranchers and absentee landowners who do not depend on ranching for livelihood and thus tend to be more tolerant—to value carnivores because they do not threaten their livelihoods (Bruskotter et al., 2017). Perhaps just as important a resource as money is access to decision-makers. In the context of wildlife management in the American West, some rural residents (e.g., those involved in agriculture, hunting and fishing) have arguably more and privileged access to decision-makers (e.g., fish and game commissions) and wildlife managers, thereby disenfranchising stakeholders (e.g., non-consumptive users) not historically involved in wildlife management decisions (Williams, 2010; Olson et al., 2015).

Finding tolerable levels of carnivore-associated risk may be the crux of current coexistence challenges. Regardless of spatial overlap and co-adaptation, coexistence as we currently operationalize it may be more likely and more widespread if acceptance of perceived risks associated with carnivores can be increased. Consider examples outside the American West, such as tigers in Hindu- and Buddhist-oriented societies or lions in African communities where they are culturally valued. In these and perhaps many other cases, culture and religion may be motivating more tolerance of carnivores (and all wildlife) and mediating associated perceptions of risk (Dickman et al., 2014; Bhatia et al., 2017; Hare et al., 2018).

Short of changing cultural and religious influences, the common key to coexistence may be in more equitable distribution of costs (e.g., risks real or perceived) and benefits (e.g., resources, positive values, and experiences) among highly diverse stakeholders. Therefore, improving best practices and policies, and assessments of such to inform lessons learned, for coexistence in the American West may require a suite of top-down and bottom-up approaches. Top-down coexistence has historically occurred via regulations (e.g., ESA) that force regulatory coexistence. As one key informant stated, "Regulatory coexistence must be in place until later swaths of public are ready to coexist. We still can't get people who would claim to like bears to use bear resistant garbage cans yet. We have a long way to go." Yet regulatory coexistence vis-à-vis the ESA shifts the loci of control away from local stakeholders. While it may be an efficient way to protect highly contentious large carnivores in the short-term, regulatory coexistence may compromise other important considerations in democratic decision-making, namely equity (Stone, 2002). Long-term sustainable large carnivore policy will likely require better ways to equitably distribute risks and resources across the spectrum of stakeholders. Additionally, an important aspect of Carter and Linnell (2016; p575) definition of coexistence is that it be "governed by legitimate institutions," which was beyond the scope of this analysis but is addressed in other studies (Serenari et al., 2018; Serenari and Taub, 2019).

Because coexistence is tenuous when only a small percentage of the population practices it, local support for coexistence is also needed. Given that, for most species of large carnivores, existence is often conservation-reliant and mortality driven by anthropogenic sources, carnivore recovery in turn "is dependent on either aiding the species' ability to adapt to the human behavior or altering the human behavior in such a way as to reduce or eliminate the impact of the threat on the species" (Kavanaugh and Benson, 2013:195). Yet ESA recovery efforts rarely aim to improve human attitudes toward carnivores. To move beyond conservation-reliance and ESA protections, federal recovery efforts need to address human behaviors (and the factors that influence them, e.g., perceptions). Additional bottom-up approaches to coexistence, according to one key informant, include "changing the perceived meaning of carnivores, moving away from their historic and symbolic associations and re-arranging the structure of wildlife management agencies to reflect changing human values" (also see Smith, 2006).

Lastly, coexistence is more likely where carnivores are not perceived as threatening livelihoods. To the extent that economies can shift from extractive, non-renewable industries to those based on sustainable tourism and outdoor recreation, Western livelihoods may become more reliant upon, rather than compromised by, carnivore existence. As the demographics of the American West shift and diversify, residents of and amenity migrants to the "new American West" may be challenging old assumptions by both living with and valuing carnivores (Robbins et al., 2009). These dynamic changes are also occurring globally, necessitated by the threats climate change and unsustainable practices pose to livelihoods everywhere and in response to increasing values for the intrinsic rights of nature by many post-modern societies (Inglehart, 1977; Batavia and Nelson, 2017; O'Donnell et al., 2018; Washington et al., 2018). By incurring any risks associated with carnivores while also deriving benefits through use (e.g., wildlife watching opportunities) and non-use values (e.g., existence and intrinsic values), the new paradigm challenges old assumptions about how to coexist with carnivores in the American West and beyond. It may come down not to resources or risk but to perspective.

AUTHOR CONTRIBUTIONS

ML and NC contributed conception and design of the study. ML performed the analysis and wrote the first draft of the manuscript. NC wrote sections of the manuscript. ML and NC contributed to manuscript revision, read and approved the submitted version.

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SUPPLEMENTARY MATERIAL

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