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Review

Toward a Synthetic Theory of Tolerance for Carnivores: Learning from a Half-Century of Research on Attitudes Toward Wolves

Jeremy T. Bruskotter [1,*], John A. Vucetich [2], Lisa Naughton-Treves [3], José Vicente López-Bao [4], Benjamin Ghasemi [5], Nicole D. Sintov [6], Tara L. Teel [7], Neil H. Carter [8], L. Mark Elbroch [9] and Adrian Treves [3]

1 Department of Community Sustainability, Michigan State University, East Lansing, MI 48824, USA
2 College of Forest Resources and Environmental Science, Michigan Technological University, Houghton, MI 49931, USA
3 Nelson Institute for Environmental Studies, University of Wisconsin, Madison, WI 53706, USA
4 Biodiversity Research Institute, CSIC–Oviedo University–Principality of Asturias, 33600 Mieres, Spain; jv.lopezbao@gmail.com
5 Independent Researcher, Austin, TX 78735, USA
6 School of Environment and Natural Resources, The Ohio State University, Columbus, OH 43210, USA; sintov.2@osu.edu
7 Department of Human Dimensions of Natural Resources, Colorado State University, Fort Collins, CO 80523, USA
8 School for Environment and Sustainability, University of Michigan, Ann Arbor, MI 48109, USA
9 Panthera Corporation, New York, NY 10018, USA; melbroch@panthera.org
* Correspondence: bruskott@msu.edu; Tel.: +1-614-595-7036

Abstract

Human intolerance is a critical factor limiting both the distributions and populations of large carnivores. Using gray wolves as a case study, we synthesize a half-century of scholarship with the aims of clarifying the conceptual foundations of "tolerance" and integrating insights from across the social sciences. Specifically, we review longitudinal studies of attitudes toward wolves and show how trends vary across the populations examined. We then identify and discuss three complementary theories that help explain variation in tolerance across individuals, social groups, and societies: (1) Risk–benefit theories illuminate how perceptions of risks, benefits, and controllability shape individuals' tolerance of carnivores; (2) Modernization theory explains societal shifts in values and shows how reduced threats from carnivores impact tolerance at the societal level; and (3) Social Identity Theory highlights how identification with interest groups (e.g., hunters, environmentalists) shape beliefs in a manner that serves to exacerbate inter-group conflicts. Linking these theoretical perspectives provides a more holistic framework for understanding why tolerance can change within populations, and why inter-group conflicts persist even as societal attitudes have become more favorable. We conclude by outlining research priorities aimed at improving our understanding of tolerance and the conditions that allow for human–carnivore coexistence.

Keywords: tolerance; coexistence; attitudes; carnivores; socio-ecological systems

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1. Introduction

Human exploitation of other species is among the most important threats to biodiversity [1,2]. While many species are hunted because of their value to humans (e.g., food, fur), some are killed directly because of real and perceived threats to human endeavors. Large

carnivores (hereafter, carnivores), in particular, are persecuted because of the perceived threat they pose to human interests, including wild and domestic animals. This mortality, whether legal or illegal, poses a persistent threat to many carnivore populations, spurring efforts to increase human tolerance for these species (hereafter, tolerance) and reduce the costs of coexistence.

Tolerance lies near the heart of a relatively new meme in conservation, i.e., "coexistence", which is rapidly becoming part of the lexicon among professionals who manage human–wildlife interactions [3–6]. Though studies on *tolerance* and *acceptance* of wildlife emerged from separate studies on human–wildlife conflict and wildlife management, they share the goal of identifying factors that lead people to be more or less accepting of wildlife and the threats posed by animals to human endeavors [7]. Scholarly conceptualizations of tolerance and coexistence evolved over the decades and trace back at least to the mid-1980s. Both ideas are arguably inherent, for example, in the concept of "cultural carrying capacity," which Ellingwood [8] defined as the maximum number of animals that can compatibly co-exist with a local human population. Cultural carrying capacity, a characteristic of a given group of people, is defined, in part, by a group's willingness to tolerate a certain number of animals (and their activities) at that place and time.

Scholarly interest in tolerance and coexistence increased dramatically since 1990 (Figure 1). The number of articles on these topics has increased by roughly 20% per year, about 4 times the rate of science publications, in general [9]. Growing interest in tolerance and coexistence has prompted recent reviews [10–14], a meta-analysis [15], and numerous calls for greater attention to conceptualization and measurement [3,4,7,16–18].

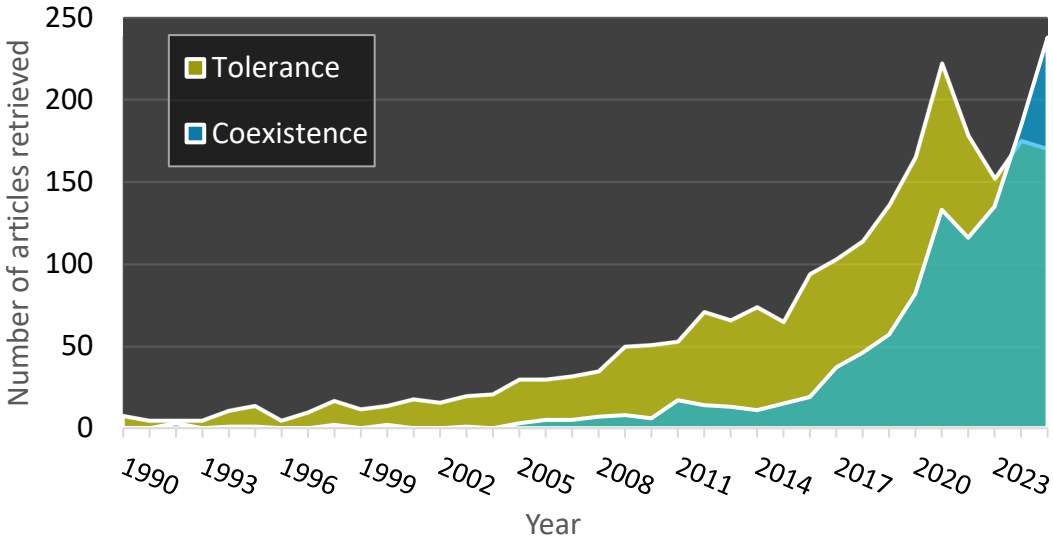

Figure 1. Papers retrieved from SCOPUS that include the terms "coexistence" or "tolerance" and "wildlife" and "conservation": 1990–2022. The coexistence trend represents the result of searching "TITLE-ABS-KEY (coexistence AND conservation AND wildlife)". The tolerance trend represents the result of searching "TITLE-ABS-KEY (tolerance OR acceptance OR attitudes AND wildlife AND conservation)". Both searches were conducted on the SCOPUS database (https://www.scopus.com).

Collectively, decades of research on attitudes toward carnivores and carnivore-related policies have provided numerous insights concerning human tolerance for wildlife—especially the identification of correlates with tolerant attitudes. Yet, our capacity to address intolerance is challenged by the lack of synthesis of these insights. Indeed, appropriately differentiating and integrating knowledge from across disciplines is a key challenge of transdisciplinary research [19]. Herein, we aim to clarify conceptual ambiguities and inform more effective policies and strategies for coexistence with large carnivores

by synthesizing theory useful for describing variation in tolerance within individuals, between social groups, and at the societal level. Collectively, these theories and the processes described help explain how and why tolerance changes—thereby offering insight for conservation action.

Conceptualizations of Tolerance

Though scholars diverge concerning key details about how to best conceptualize and measure tolerance [4], there appears to be a general consensus that tolerance has both attitudinal and behavioral components [11,16,20]. More specifically, tolerance has been described as a passive behavioral state [21] that includes a "willingness. . .to absorb the extra potential or actual cost of living with wildlife" [22] (p. 138). In practice, however, the term tolerance has been applied as a kind of catch-all term to refer to a variety of internal (psychological) phenomena, including attitudes, behavioral intentions, and prior behaviors that affect wildlife both directly (e.g., shooting, poaching) or indirectly (e.g., political action) [7,12]. Because the majority of studies—especially early studies—measure *attitudes* towards species or their management, we begin with a brief overview of the psychology of attitudes. We provide definitions for all key concepts discussed in this paper in Table 1.

In psychology, *attitudes* refer to individuals' tendencies to evaluate entities with favor or disfavor [23]. The attitudes that one holds toward a given entity are shaped both by individuals' direct experiences with that entity, as well as social interactions that convey information about an entity, including group expectations for appropriate attitudes toward that entity [24]. In the broad literature on tolerance for wildlife, the types of attitudes assessed may pertain to direct evaluations of species [25,26], evaluations of management or conservation actions (e.g., reintroduction of a species, killing a species), (e.g., [27–29]), or preferences for species' population size or population changes (e.g., "wildlife acceptance capacity"; e.g., [30,31]). While these various kinds of attitudes tend to be strongly related statistically [32], they are conceptually distinct. For example, it is possible for an individual to hold very positive attitudes toward a species but believe the species to be locally overpopulated and therefore prefer management actions aimed at reducing its abundance.

Table 1. Key concepts and their relations with literature on tolerance for wildlife.

Concept and Definition	Relation with Tolerance
Value orientations—Reflect the influence of cultural ideology on beliefs about how humans should ideally interact with nature. [a]	Value orientations affect subsequent judgments, helping individuals adjudicate how they (individually) and society should relate and interact with wildlife.
[a] Adapted from: Manfredo, M.J. *Who Cares about wildlife? Social science concepts for exploring human–wildlife relationships and conservation issues*. Springer: New York, NY, USA. 2008. [33]	
Social Identity—The part of one's self-concept derived from their membership in a social group and the value or significance one attaches to that membership. [b]	Through interactions with group members, individuals learn what values, attitudes, and behaviors are ideal for that group. The desire for belonging provides a motivation to conform to in-group expectations—including how we should relate and interact with wildlife.
[b] Adapted from: Tajfel, H.; Turner, J.C. An integrative theory of intergroup conflict. In *The social psychology of intergroup relations,* Austin, W. G., Worchel, S., Eds.; Brooks/Cole: Monterey, CA, USA, 1979, pp. 33–48. [34]	
Risk and Benefit Perceptions—Intuitive judgments about the likely outcomes associated with a potential hazard. [c]	Individuals tend to be less tolerant of hazards viewed as risky and more tolerant of those viewed as beneficial.
[c] Adapted from: Slovic, P. Perception of risk. *Science* **1987** *236*, 280–285. [35]	

Table 1. *Cont.*

Concept and Definition	Relation with Tolerance
Attitude—Describes a tendency to evaluate an entity or object with favor/disfavor. [d]	Individuals tend to be more tolerant of entities (whether animals or humans) that they evaluate favorably.
[d] Adapted from: Eagly, A.H.; Chaiken, S. *The psychology of attitudes*. Harcourt Brace College: Fort Worth, TX, USA. 1993. [23]	
Coexistence—A state involving the persistence of self-sustaining large carnivore populations in human-dominated landscapes whereby humans and wildlife co-adapt to living in shared areas through behavioral changes. [e]	Coexistence requires collective behavioral changes (adaptation) intended to promote the persistence of wildlife populations.
[e] Adapted from: Chapron, G.; López-Bao, J.V. Coexistence with large carnivores informed by community ecology. *Trends Ecol. & Evol.* **2016**, *31*, pp. 578–580. *AND* Carter, N.H.; Linnell, J.D. Co-adaptation is key to coexisting with large carnivores. *Trends Ecol. & Evol.* **2016**, *31*, pp. 575–578. [36,37]	
Tolerance/Acceptance—Describes a psychological willingness to absorb real and perceived costs of wildlife, including refraining from engaging in behaviors that cause harm. [f]	**NA**
[f] Adapted from: Bruskotter, J.T.; Singh, A.; Fulton, D.C.; & Slagle, K. Assessing tolerance for wildlife: clarifying relations between concepts and measures. *Hum. Dimens. Wildl.* **2015**, *20*, pp. 255–270. *AND* Kansky, R.; Kidd, M.; Knight, A.T. A wildlife tolerance model and case study for understanding human wildlife conflicts. *Bio. Cons.* **2016,** *201*, pp. 137–145. [7,22]	

Attitudes are 'held' internally—they are phenomena of the mind, but they can be expressed behaviorally via conscious choices, such as voicing one's opinion in a public forum (see generally, [33]). Behavioral expressions of tolerance can take many forms, such as expressing positive or negative attitudes in social media, becoming politically engaged on matters pertaining to carnivores, and killing carnivores [21]. Numerous human behaviors contribute to the death or displacement of wildlife; however, the phrase "intolerant behaviors" is generally reserved for behaviors that are undertaken *intentionally* to harm an individual or population [7]. Thus, whether any instance of regulated sport hunting would be considered intolerant behavior depends, in part, on the hunter's motivation [38,39].

Importantly, decades of research on attitude–behavior consistency suggest that even where attitudes align with risk and benefit perceptions, individuals may not act accordingly [40]. Such research indicates, for example, that a variety of factors (such as perceived group norms) can moderate the relationship [41]. Thus, a person with intolerant attitudes may choose not to act in an intolerant manner in situations where they feel their views are not shared by those around them.

To date, the study of 'tolerance' for wildlife has been pluralistic—it has invoked a variety of related concepts (e.g., attitudes, norms, values, risk perceptions, social trust, etc.), associated theories, and methodological approaches [4,21]. Importantly, we do not advocate here for any specific conceptualization of tolerance. Rather, our intent is to show readers the breadth of concepts that are sometimes referred to as 'tolerance' (or at least indicators of tolerance) in the scholarly literature and policy-making discourse.

2. Understanding Changes in Tolerance: A Case Study of Attitudes Toward Wolves

Gray wolves (*Canis lupus*) have attracted considerable attention from scholars over the past several decades, providing an opportunity to examine changes in attitudes—an indicator of tolerance— over time. We conducted multiple searches of the SCOPUS and Google Scholar databases and consulted with other scholars in our field, ultimately identi-

fying just 10 peer-reviewed studies that (a) quantitatively evaluated changes in attitudes towards wolves that occurred over a specific period of time, and (b) had sufficient sample sizes to provide a 5 percentage points margin of error at the 90% confidence level for the primary population of interest (Figure 2). Importantly, these studies vary considerably in terms of their approach. Most studies used repeated cross-sectional surveys, whereby separate samples were drawn from the same study population at multiple time points, whereas a few studies used repeated measures, whereby the same subjects were measured on multiple occasions. And some studies mixed the two methods by adding new respondents to existing panels. These methods differ with respect to the types of change they can detect. Repeated cross-sectional surveys are best for detecting population-level changes (e.g., changes due to intergenerational replacement), whereas repeated measures are used to detect individual-level (i.e., within-subjects) changes [42].

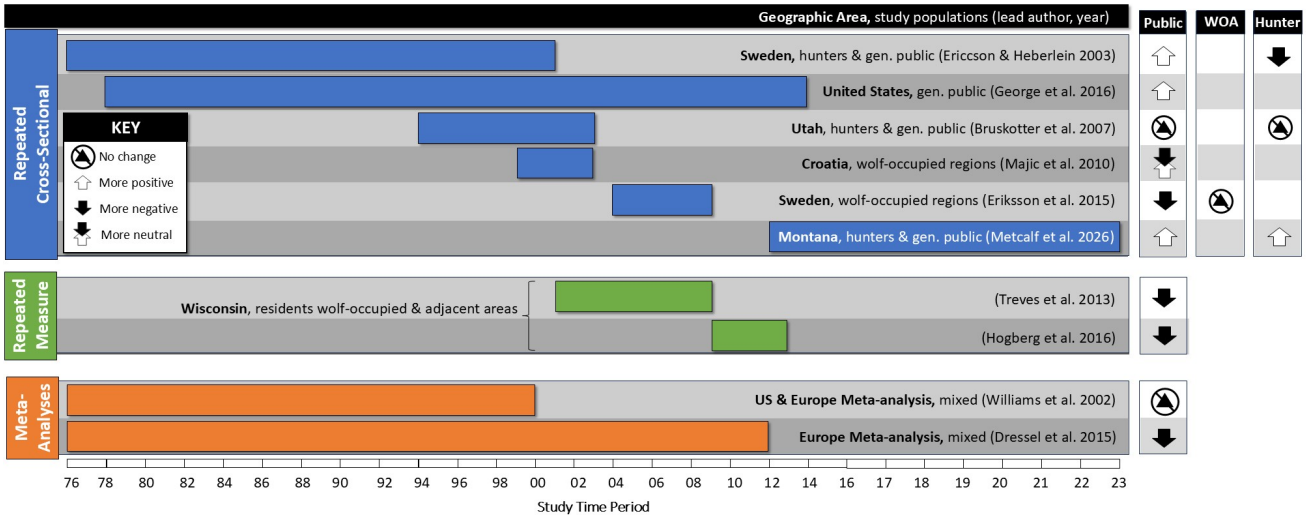

Figure 2. Peer-reviewed articles assessing attitudes towards wolves over time. The ends of each bar indicate the two times at which data were collected; WOA refers to 'wolf-occupied' areas [25,43–51].

Two long-term (>20 years) repeated cross-sectional studies of residents of Sweden [43] and the U.S. [25] found that attitudes toward wolves had become more positive since the 1970s. Indeed, the more recent study found that the proportion of Americans expressing positive attitudes towards wolves increased by more than 40% between surveys conducted in 1978 and 2014 [25]. Similarly, in Sweden, Ericsson and Heberlein [43] found an increase in favorable attitudes towards wolves among the general public from 1976 (when no wolves existed in the country) to 2001 (when about 100 wolves resided in Sweden); however, those identifying as hunters exhibited the opposite trend (becoming more negative). And a more recent, short-term (2004–2009) study found no change within the general population of Swedish residents; however, they found a decline in positive attitudes among residents living in wolf-occupied municipalities [44]. Other repeated cross-sectional surveys exploring attitudes towards wolves among general publics have shown no change (comparing 1994 and 2003 in Utah, U.S.; [45]), shifts away from extreme attitudes (positive or negative) toward neutrality (comparing 1999 and 2003 in Croatia; [46]), and most recently, increased *tolerance* for wolves among both hunters and the general public of Montana [47].

The most powerful studies for detecting change within individuals use a repeated-measures design whereby the same respondents report their attitudes on at least two occasions. Only two studies have employed this design, and both surveyed residents of Wisconsin (U.S.) living within wolves' geographic range and adjacent areas. The first study found that respondents expressed more negative attitudes toward wolves and a greater willingness to poach wolves over a 5–8 year period (2001–2009), during which time wolf

abundance increased, the issue received intense and predominantly negative media attention, and the killing of wolves was liberalized [48]. This study also found that increased negativity was not limited to hunters or dependent upon having directly experienced a loss of livestock or pets due to wolves. A follow-up study of the same sample in 2013 supported findings from the first analysis and found significant declines in positive attitudes toward wolves among respondents. However, in this case, post hoc analyses revealed the decline was limited to male subjects and hunters [49].

The complicated impression given by these studies is reinforced by meta-analytic studies that consider change over time. A 2002 meta-analysis of studies conducted in the U.S. and Europe found no evidence of change from 1972 to 2000 [50], but a 2012 meta-analysis of European studies found evidence that attitudes toward wolves became more negative since 1976 [51]. Specifically, Dressel and colleagues [51] found that positive attitudes toward wolves declined where wolf populations were long-established. However, inferences drawn from meta-analytic techniques are hampered by the use of a wide variety of measures of attitudes (e.g., beliefs about wolves, direct evaluations of wolves or wolf reintroduction, wildlife acceptance capacity), which may not be equivalent, as well as differences in the populations studied (i.e., geographic state or region where attitudes were assessed), which complicates comparisons of the cross-sectional studies as well.

Other details of these studies may be useful for understanding inferences that can be made about how and why attitudes toward wolves change among different groups or populations. Two of the three studies that found attitudes toward wolves had improved were much longer in duration and targeted the general publics of two highly urbanized countries (i.e., the U.S. and Sweden), where the vast majority of residents would have little experience with or knowledge of wolves. The positive changes found in these general population studies stand in contrast with studies focused on people living within the geographic range of wolves, near wolf habitat, or those who identified with groups in direct competition with wolves over game populations (i.e., hunters). These studies generally found that attitudes toward wolves became more negative over time among these specific populations [44,48,49]. Importantly, these studies were conducted in the same countries, Sweden and the U.S., where the general populations were found to be more positive. In support of this finding, a recent systematic review of studies of attitudes found that people in areas with a continuous wolf presence tended to hold more negative views towards wolves than those living in areas with no wolves or where wolves had recently returned [52]. However, this finding directly conflicts with the cross-sectional study from Montana that found increased "tolerance" among both the general public and hunters [47]. Importantly, however, this study's single-item measure of *tolerance* differed substantially from the types of measures employed in the other studies mentioned.

A tentative conclusion that could be drawn from these studies is that attitudes toward wolves appear to be improving at the societal level—at least among those who are least likely to be negatively impacted by wolves. In contrast, they generally appear to be declining among those identifying with groups most likely to be negatively impacted, such as hunters. This interpretation is reinforced by additional cross-sectional studies showing that, consistent with the NIMBY (not-in-my-backyard) phenomena, attitudes toward wolves tend to correlate negatively with their presence [53], positively with one's distance from their range [54], and negatively with activities that predispose humans toward some risk (e.g., raising livestock or hunting) [50]. The exceptions are the aforementioned Montana study [47] and a Utah study, which found no changes in attitudes among the general population, rural residents, or hunters over a 9-year time period [45]. However, in contrast with the Montana study, both Utah surveys were conducted at times when no wolf populations were present in the state.

Generally, we tentatively infer that negative attitudes toward wolves (a key indicator of intolerance for the species) are more likely to increase over time where wolves are present, at least among those belonging to or identifying with groups more likely to be negatively impacted. This inference may seem intuitive—even obvious— but it conflicts with the general assumption often made by management agencies and some scholars, i.e., that attitudes toward wolves are improving [55]. Indeed, perhaps the more interesting question is why some studies show that attitudes toward wolves improved at all? To address this question, it is useful to distinguish between different types of variation (e.g., within individuals, between groups) that can arise from very different processes. That is, the reason groups of people—say those living in a particular geographic area—exhibit different attitudes over time may be different from the reasons individuals exhibit different attitudes over time. We turn next to identifying theories useful in understanding these differing sources of variation, thereby moving us appreciably toward synthesis.

3. Explaining Tolerance Across Individuals: Risk and Benefit Judgments

A common measure of tolerance asks individuals whether they would prefer a local population of a species to decrease or increase [31,56]. In effect, such judgments represent one's attitude toward population change. Researchers quickly recognized that such attitudes depend, to some degree, on how individuals assess the risks associated with a species [31,57,58]. When species are perceived as threatening—that is, potentially risky or costly, tolerance tends to be lower (i.e., attitudes favor population reductions). Additional support for this general notion is found in the literature showing that support for killing carnivores in response to conflict (another measure of intolerance) tends to increase with the perceived severity of the threat [30,59–61]. Conversely, numerous studies indicate tolerance tends to be higher when species are perceived as beneficial [17,62–64].

Large carnivores can be considered a kind of hazard. Research on the acceptance of hazards provides a general theoretical framework for understanding why acceptance (or tolerance) of a hazard varies across individuals [10]. In general, this research indicates that perceived benefits tend to be stronger predictors of acceptance of hazards than perceived risks [65]—a finding replicated in some studies of tolerance for wildlife (e.g., [63]).

Some work also highlights the impact of different kinds of benefits on tolerance for wildlife; specifically, Marino and colleagues [18] found 'intangible' (i.e., non-monetary) benefits to be more important predictors of tolerance than tangible, monetary benefits for many cases involving the tolerance of wildlife. Similarly, Ghasemi et al. [29] found that measures of societal benefits were more important than personal benefits in explaining support for restoring cougars and red wolves.

Although these studies generally indicate that risk-benefit judgments are useful for explaining variation in tolerance across individuals, they also raise the question: why do such judgments vary to begin with? Research shows both perceptions of risks and benefits are influenced by various other factors, such as the extent to which interactions with a species are viewed as 'controllable' and the extent to which wildlife managers are perceived as trustworthy, in the sense of being competent and sharing similar values [10]. Importantly, these factors also represent mechanisms by which tolerance could be manipulated. Thus, Slagle et al. [64] used an experimental approach to show that tolerance for black bears (Ursus americanus) could be increased by providing information on the benefits of bears, along with information about how to avoid the risks of living near bears (thereby making risks more 'controllable'). Similarly, Guerrero [66] found that farmers' tolerance for pumas and jaguars increased when the farmers living in their range were provided tools to protect livestock—even in cases where the tools proved ineffective. Other factors, such as affect (or emotional reactions to carnivores), as well as trust in wildlife management agencies,

can also influence tolerance of carnivores, particularly in situations where familiarity with the hazard is low [67,68]. Beyond organismal perceptions (e.g., attitudes, risk-benefit perceptions), research in moral psychology and decision science reveals that ethical factors can play an independent role in shaping attitudes and behavioral intentions [69,70]. Moral considerations can influence how we perceive costs and benefits, especially when we lack direct knowledge of the consequences [71,72]. An emerging line of research demonstrates the effect of ethical considerations on tolerance. For instance, Hermann and Menzel [73] reported that framing wolf recovery as an ethical imperative to restore the species increased support for their recovery among secondary school pupils in Germany. Also, Lute et al. [74] showed that those who attributed intrinsic value to wolves expressed higher tolerance for their presence in Michigan (U.S.).

4. Explaining Variation Across Groups

Although no longitudinal data existed at the time, by the mid-1990s, the idea that attitudes toward wolves had improved in the U.S. had become prevalent among many conservationists. Indeed, a 1996 review argued, "In the U.S. and Canada attitudes toward wolves and wilderness changed greatly during the course of the twentieth century" [75] (p. 979). Kellert and colleagues explained the purported change as resulting, in part, from increased rarity of wolves, but also from "an expansion of knowledge" and a "profound transition in values" that reflected a new understanding of ecology [75]. This thesis was based, in part, on studies showing that attitudes toward wolves and coyotes were positively associated with individuals' levels of education and general knowledge of animals [26]. Indeed, in their meta-analysis, Williams et al. [50] found that 18 of 20 studies reported attitudes toward wolves as being positively related to education levels. Moreover, they found attitudes tended to be associated with higher levels of income and residency in urban settings. However, these studies provided little insight into why this is the case—they merely described differences across education or income levels.

4.1. Shifting Social and Economic Conditions

A long-term program of research in the U.S. helps address this deficiency. Research on wildlife value orientations provides evidence that Americans' beliefs about ideal relationships with wildlife have been shifting from domination toward mutualism orientations [76]. While domination refers to the idea that wildlife should be viewed primarily as resources to be used and managed for human benefit, mutualism views wildlife through a more egalitarian lens, whereby wildlife are part of one's moral community and deserving of care and compassion [77]. Importantly, this shift from domination to mutualism is associated with the process of modernization, as indexed by increased income, education, and urbanization [78]—the same factors found in many studies to be associated with attitudes toward wolves at the individual level. Effectively, this research suggests that as nations modernize, social changes prompt the formation of new value orientations, effectively allowing groups to adapt to changing conditions.

Studies have shown that domination and mutualism orientations are associated with a wide variety of attitudes, beliefs, and behaviors relevant to carnivore conservation at the individual level [76,78–80], and wolf conservation more specifically. For example, wildlife value orientations have been shown to be associated with attitudes toward wolves [81], the management of wolves [82], as well as perceived risks of wolves [83]. Research further indicates that U.S. residents who exhibit stronger mutualism orientations are more likely than other residents to oppose lethal control of wolves that attack livestock [84], one indicator of increased tolerance.

Similarly, an earlier study found that mutualists (individuals who score high in mutualism and low in domination) tended to express strong opposition to the reduction in wolf numbers to enhance opportunities to hunt deer and elk, while those with a strong domination orientation were more accepting of this practice [79]. Furthermore, research in Washington state (U.S.) showed support for wolf recovery was greatest in counties with more mutualists, where there was also greater resistance to lethal removal and recreational hunting of wolves [80].

A related line of research suggests that intolerance for wolves can arise in rural communities when socioeconomic conditions decline relative to urban areas. This research emphasizes how changes associated with modernization can be viewed by some rural communities as threatening to traditional rural life and livelihoods [85–87]. Krange and Skogen [87] explain that when new perspectives challenge traditional land uses, "these developments are perceived as threatening" to rural populations. Therefore, intolerance can be viewed as a kind of resistance to social changes perceived as being imposed upon rural communities by outsiders [85]. Similarly, Wilson [88] emphasized that the controversy over wolves in the western U.S. pitted traditional "Old West" values against those who held a new vision for the West and were thus seen as threatening to local traditions and livelihoods.

Relatedly, urbanization can also shift political power in geopolitical units with proportional representation. In much of the U.S., for example, rural communities are experiencing long-term population declines [89]. The loss of political power (and associated control over one's circumstances) may, in turn, prompt those living in regions to 'lash out' against those they view as responsible, or to resist changes linked to 'outside forces'. One might expect such actions to be particularly prevalent in times of heightened conflict, such as during high-stakes elections.

Collectively, these studies indicate that tolerance for carnivores is— or at least can be—rooted in more fundamental value orientations that are themselves driven by societal modernization. Moreover, another related theory of values helps to identify the underlying mechanisms involved. Specifically, Inglehart and Welzel [90] hypothesized that modernization's effect on values (at the societal level) was due to a reduction of 'existential threats' that allowed societies to shift their concerns from meeting basic human survival needs to focusing on higher-order concerns (e.g., social affiliation, self-expression). Accordingly, Manfredo et al. [78] found that increased affluence (measured by gross domestic product per capita) in U.S. states was strongly and positively associated with changes in mutualism orientations in these states.

But this is not the only mechanism through which modernization could impact tolerance for carnivores. Modernization also affects how people and animals are distributed on the landscape, and therefore, how they interact. For example, as human populations urbanize, people are less likely to encounter large carnivores, which ultimately reduces both the real and perceived risks these animals pose [91], thereby making them easier to live with. The reduction in societal-level actual and perceived threats posed by carnivores provides a conceptual link between processes occurring at the societal (modernization) and individual (e.g., risk-benefit assessment) levels. Linking social and individual-level processes.

Beyond modernization's effect on value orientations, associated social changes could also influence which social groups people seek out and identify with. Consider this: in 1900, approximately 59% of laborers in developed countries worked in agriculture; by 1970, this number had shrunk to 23% [92]. According to the U.S. Bureau of Labor Statistics, less than 1% of the US population is employed in agriculture today, and these changes are tied directly to the technological modernization of agriculture [93].

These changes are important because attitudes about wildlife vary with the degree to which one identifies with particular social groups [50]. Indeed, both meta-analyses of

attitudes toward wolves found that ranchers and farmers tended to hold the most negative attitudes toward wolves [50,51]. Thus, to the extent that modernization is responsible for shifting people from working in agriculture to other occupations, it may have helped improve attitudes toward wolves across numerous countries.

4.2. Tolerance and Social Identities

Tolerance for wolves also varies among those who self-identify as members of various other groups beyond agriculture, including hunters, environmentalists, and animal welfare advocates [32]. A simple, rational explanation for these associations is that these groups have different interests. For example, wolves and other large carnivores represent potential threats to the livelihood of livestock owners, and they potentially compete with some types of hunters for the same prey; thus, because their interests are potentially threatened, it follows that people who identify as members of these groups tend to hold more negative attitudes toward wolves.

However, while different interests are often a source of conflict over natural resources, interest alone is insufficient for understanding why groups come to hold such divergent views. An example serves to illustrate. The aforementioned pattern (whereby attitudes are associated with membership in a particular group) would appear to be explainable entirely by individual-level processes (e.g., I am a hunter, wolves prey on game populations, therefore I am less tolerant of wolves). However, decades of research on intergroup conflict suggest there are also underappreciated group-level processes at work (e.g., I identify with a group of hunters, these hunters dislike wolves, I am inclined to adopt their views).

Social identity theory, in particular, provides valuable insights concerning how individuals relate to groups and the processes by which group identification can impact members' attitudes and beliefs. Turner et al. [94] argued that individuals evaluate the importance of their ingroups by contrasting them with relevant outgroups. Through interactions with various group members (both in and out), group members may— to the extent that they identify with a group—form "prototypes" or idealized representations of social group members. A prototype "...not only describes what it is to be a group member, but also prescribes what kinds of attitudes, emotions, and behaviors are appropriate in a given context" [95] (p. 209). Thus, when a group identity is activated in the memory of a particular individual, group prototypes provide that individual with information about ideal ways of thinking and behaving, exerting pressure to conform to the expectations of the ingroup. These perceptions may be further reinforced through group interactions in which individuals receive feedback (in the form of sanctions) from other group members for conforming or not conforming to expected ways of thinking and acting.

In a large sample of U.S. residents, Carlson et al. [81] recently showed that four types of social identities (i.e., hunters, farmers/ranchers, environmentalists, and animal rights advocates) were all related to at least one attitudinal measure of tolerance for wolves, even after numerous other factors were controlled. Likewise, Bruskotter et al. [96] found that identifying with these (and other) interest groups was moderately associated with both mutualism and domination orientations across three separate studies. Collectively, these studies suggest that the processes of (i) identifying with various groups, and (ii) adopting prototypical attitudes, beliefs, and behaviors of that group, may be useful for explaining how people come to hold divergent attitudes and beliefs about wolves and other wildlife (also, see [97,98]).

5. Discussion: Toward a Synthesis

Much research on tolerance is conducted from the narrow perspective of one discipline and without regard for other academic perspectives. This 'siloing' of perspectives can

create the illusion that the various theories for understanding tolerance are in conflict with one another, when they may be complementary. Indeed, our brief review shows how complementary insights are provided by three of the dominant perspectives on tolerance; i.e., research on (1) the acceptance of hazards, (2) modernization and value change, and (3) social identity theory. Wildlife value orientations—shown to be related to societal-level forces such as modernization—can help explain how shifts in social conditions over time can affect how people judge interactions with wildlife, effectively promoting or inhibiting tolerance within communities. Social identity theory provides insights into the role relevant interest groups can play in promoting differing ideas about carnivores, including the extent to which they pose a risk, and how carnivores should be treated/managed. The psychology of risk and personal decision-making helps explain how individuals come to formulate judgments concerning whether carnivores are acceptable and what kind of actions and management are appropriate. The unique contribution of each perspective helps us to view tolerance from a more holistic perspective.

Viewing tolerance from this holistic perspective, in turn, helps explain why studies on temporal changes in attitudes have shown such divergent findings. That is, urbanization and economic modernization are likely promoting more positive views of carnivores at the societal level, especially in countries where the majority of the human population now resides in urban environments [91]. We emphasize that changing social conditions can impact both social (or inter-group) conflicts, as well as the material conflicts between people and wildlife. That is, changing social conditions may affect attitudes through their impact on more fundamental values, creating social conflict among groups with competing values and preferences for management. Furthermore, changes in social conditions can also effectively remove people (those who move from rural to urban settings) from any material threat posed by carnivores.

However, we should not expect the same changes in rural communities where carnivores are present or likely to recover, especially where those communities feel threatened by economic decline or the loss of cultural traditions [85]. In such places, the combined effects of perceived threats (e.g., carnivore predation on wild and domestic prey), perceived disadvantage (especially relative to outgroups), and broader fear of social changes that are perceived to threaten traditional lifestyles could help explain why wolves tend to be viewed more negatively by individuals and interest groups within such communities. In fact, the literature on values suggests these same types of communities—those 'left behind' by the forces of modernization— tend to be less tolerant of carnivores [78].

Paradoxically, the dynamic described herein suggests that the very places best suited for reducing human-carnivore encounters (i.e., areas with low human densities) are also likely to be the places where intolerance is greater. These processes also help explain why large-scale, cross-sectional surveys can show increasingly positive attitudes towards wolves, while studies conducted in areas with wolves tend to show the opposite trend. However, nearly all of the studies reviewed here target general populations in wealthy, developed nations. It is yet unclear if and how attitudes are changing in less developed nations and among indigenous peoples. Likewise, the extent to which the theories reviewed here generalize among less developed nations or to indigenous contexts is largely unknown. Nevertheless, while we might expect the value-orientations, identities, and perceptions that are at work to differ across cultural contexts, we anticipate that the basic processes (e.g., reasoning from abstract values to more concrete judgments) involved in rendering such judgments will be similar. This implies that, for example, among some groups (e.g., indigenous peoples), identifying with a particular group (e.g., hunters) may reinforce perceptions about wildlife that differ markedly from those identifying with the same type of group in a different culture.

Moving forward, researchers should develop and empirically test models that capture the interplay of modernization, value orientations, risk-benefit perceptions, and social identity processes to predict tolerance across different contexts. For example, cross-regional studies could examine how the process of modernization interacts with local economic decline to shape tolerance in rural vs urban communities. Research is also needed to explore how beliefs about and attitudes toward carnivores are affected by identification with key interest groups over time (e.g., via long-term panel studies), especially during periods of escalating impacts from carnivores or policy changes, such as carnivore reintroductions. Doing so could help disentangle individual and societal sources of change in tolerance. Likewise, assessing tolerance outcomes across different levels—individual, group, community—and contexts could help determine at which level(s) theories have the greatest predictive power, and therefore, the most potential for shaping management outcomes related to coexistence.

Establishing causal relationships between tolerance and processes occurring within and across levels is challenging, as inferences may be confounded by a number of factors. Indeed, much of the work on tolerance and modernization (at least in wildlife contexts) draws on cross-sectional studies, where the directionality of relationships is unclear. We recommend that future research utilize rigorous causal inference methods. For example, studies can use policy changes (e.g., carnivore reintroduction, compensation schemes) or sudden ecological shifts as "treatments" and compare affected and unaffected groups/areas using difference-in-differences, regression discontinuity, or instrumental variable approaches. Likewise, a repeated-measures design that tracks the same individuals or communities over time helps identify temporal ordering and rule out reverse causality. While we expect such designs to yield new insights, we also acknowledge that the processes that lead individuals or societies to act in more or less tolerant ways could be affected by a variety of factors, such as historical policy trajectories and governance structures that make each context unique.

Bridging social science theories of tolerance with animal ecology could enable integrative social-ecological systems approaches, linking changes in human attitudes, values, and social identities to patterns of carnivore behavior, distribution, and population dynamics. For example, longitudinal and experimental designs can reveal whether changes in human attitudes (e.g., improved tolerance following education campaigns or compensation policies) directly lead to measurable changes in carnivore abundance, behavior, or habitat use. Conversely, monitoring carnivore populations can also uncover feedback effects on human perceptions.

Research on intervention approaches to foster tolerance is still in its infancy [64,99,100], and further efforts are sorely needed. Such efforts can be guided by broader research on how incentives, messaging, and other techniques affect attitudes, intentions, and behavior. Indeed, though not focused on carnivore tolerance explicitly, broad studies in the social sciences support the use of incentives and various communication techniques across environmentally relevant contexts [101–105].

By combining longitudinal data on social change and group identity with ecological monitoring of carnivore movements and risk landscapes, scholars can gain a holistic understanding of how human and animal systems co-adapt in response to management interventions and environmental change.

Finally, though our efforts focus on synthesizing insights from three disparate theories, we anticipate that numerous theories from across a variety of disciplines could provide additional insights. Our effort was not intended to provide a comprehensive synthesis, but rather, to demonstrate how these theories complement (as opposed to compete with) one another. In so doing, this synthesis moves us appreciably toward a more holistic view of tolerance. Efforts to better understand and integrate how ethical judgments (e.g., the

recognition of a species' intrinsic value) impact tolerance and to determine how these judgments vary across social groups may be particularly useful in future syntheses.

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