Stacks

“Although elephants bring problems, they also bring benefits:” The complexities of human-wildlife coexistence

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Human Dimensions of Wildlife | Human-Wildlife Interactions

Abstract

As wildlife populations decline globally, there is a growing need to discover ways that humans and wildlife can sustainably coexist in shared landscapes. One way to assess the potential for human-wildlife coexistence is by examining human attitudes, perceptions, and tolerance of wildlife. However, the relationships between these interlinked concepts are not always clear. Furthermore, much of the research on human tolerance of wildlife

to date fails to assess differences across species. Here, we use a novel application of ethnoecological methodologies (including free-listing and pile-sorting) to assess local people's attitudes toward and tolerance of a variety of wildlife species. We conducted our study in Mukungule Game Management Area outside North Luangwa National Park in Zambia.

Abstract photo. *Bull elephant on the riverbank in Zambia.*

Our results reveal significant nuance in people's attitudes toward and tolerance of local wildlife. We found that people generally like local wildlife, but the positive attitudes did not always translate into tolerance of those wildlife species. Elephants (*Loxodonta africana*) were collectively considered the most liked, disliked, beneficial, and harmful (according to Smith's Salience scores from free-listing), and 32 percent of participants were tolerant of elephants. We highlight the importance of assessing determinants of tolerance within a local and species-specific context.

Keywords: attitudes, community-based natural resource management, North Luangwa National Park, wildlife tolerance, Zambia

Introduction

Wildlife populations are declining drastically worldwide due to anthropogenic threats including overexploitation, land cover change, invasive species, climate change, and even human-wildlife conflict (Leclère et al., 2020; Nielsen et al., 2021; Nyhus, 2016). Negative interactions between humans and wildlife constitute conflict which can have consequences for humans (i.e., crop raiding, livestock predation, attacks on humans), wildlife (i.e., habitat degradation, poaching, over-exploitation) or both (i.e., disease transmission) (Kahler and Gore, 2015). Human-wildlife conflict has resulted in significant economic losses, adverse human health impacts, and the loss or decline of wildlife species (Nyhus, 2016). These conflicts are highly complex and pose a major threat to wildlife conservation worldwide, particularly surrounding protected areas (König et al., 2020). Mitigating conflict and promoting coexistence is indispensable for conserving wildlife and improving human lives/livelihoods (König et al., 2020; Marchini et al., 2019). For humans and wildlife to coexist in the same physical spaces, humans must be willing to accept or tolerate the presence and potentially the costs associated with wildlife.

Indigenous people and local communities are the owners and de facto managers of many protected areas and regions designated as biodiversity hotspots (ICCA Consortium, 2021). Previous conservation efforts that exclude local people or villainize them have largely proven ineffective for achieving the desired conservation outcomes and may have negative social outcomes (Kashwan et al., 2021). Furthermore, these exclusionary approaches are often viewed as illegitimate by local people which may discourage conservation behavior and ultimately undermine local support needed for long-term conservation success (Siurua, 2006). There is growing recognition of the need to respectfully collaborate with Indigenous people and local communities toward the goal of conserving biodiversity, but little research on how this should be done in practice. Conservation researchers and practitioners need to acknowledge the complexity of local knowledge, perceptions, attitudes, and behaviors toward wildlife and empower local people to determine conservation interventions that are both effective and culturally appropriate.

One key aspect of local perceptions and attitudes that is poorly understood is tolerance of wildlife. Tolerance can be defined as intention to behave in a way that allows wildlife to live in the area, while intolerance is an intention to behave in a way that prevents wildlife such as retaliatory or preemptive killing of dangerous wildlife, over-exploitation, and/or habitat manipulation meant to exclude wildlife (Bruskotter et al., 2015; Kansky et al., 2016). Tolerance and acceptance are based on a complex combination of factors including attitudes, values, norms, beliefs, socio-economics, political contexts, media, past experiences, and cultural identity (Brenner and Metcalf, 2019; Kansky et al., 2016; Zimmermann et al., 2020). While attitudes can help predict tolerance and other intended behaviors, the relationship is not exact and may not be consistent across time, space, or species.

Attitudinal studies have been used to predict tolerance for wildlife (e.g., Kansky et al., 2014). Studies on tolerance are then used to predict actual behaviors and inform interventions aimed at behavioral change related to conservation. However, an overemphasis on attitudes can be problematic because they are challenging to study and poorly designed methods or analyses may lead to erroneous conclusions (Whitehouse-Tedd et al., 2021). Attitudes on specific topics are better at predicting specific behaviors than general attitudes (Ajzen and Fishbein, 2005), yet conservation research often focuses on general attitudes toward wildlife (e.g. Störmer et al., 2019). Research from Kenya shows that people were more likely to have positive attitudes toward charismatic species and negative attitudes toward non-charismatic species, yet this relationship did not hold for lions (Pinho et al., 2014). In a meta-analysis, Kansky et al. (2014), found more positive attitudes toward elephants (65%) than primates (55%), ungulates (53%), or carnivores (44%). Furthermore, overall positive attitudes toward wildlife might mask negative attitudes toward individual species or unwillingness to live with wildlife that are liked in general (the “not in my backyard” concept) (Sweet et al., 2024). Therefore, it is important to examine species-specific contexts rather than solely looking at attitudes toward wildlife in general.

To address these gaps, we evaluated these interrelated concepts of wildlife tolerance, attitudes and emotional responses toward wildlife, wildlife-related costs or benefits, personal experiences, and demographics in a local community outside North Luangwa National Park in Zambia. We

also explore how these concepts vary for different species recognizing that even how tolerance is determined may vary depending on the species in question. We used semi-structured interviews that incorporate ethnoecological methods of free-listing, pile sorting, and ranking to uncover the nuances in attitudes, emotional responses, perceptions, knowledge, and tolerance of wildlife species. By better understanding how people determine their willingness to tolerate wildlife species, we can work with local communities to design more effective and culturally acceptable conservation strategies. Understanding the inter-related aspects of human-wildlife coexistence simultaneously and across multiple species can help inform effective conservation strategies and interventions to reduce conflict and promote coexistence globally.

Methods and Materials

Study area

North Luangwa National Park is home to high levels of biodiversity and an abundance of wildlife, particularly along the Luangwa River. North Luangwa National Park is surrounded by four Game Management Areas (GMAs), Musalangu to the north and east, Lumimba to the southeast, Munyamadzi to the south, and Mukungule to the west (Figure 1). GMAs are specifically zoned for wildlife utilization and unlike National Parks they allow for mixed human and wildlife occupancy. In GMAs wildlife is owned by the state and utilization is allowed through the purchase of a specific hunting license or permit (Lewis et al., 1990). Human-wildlife conflict is common in the GMAs surrounding North Luangwa National Park and manifests in crop loss, livestock predation, or direct threats to humans (Esmail et al., 2014). In the 1980s North Luangwa experienced heavy pressure from commercial poaching which led to the local extinction of black rhino and severely decreased populations of elephants. After efforts to control illegal hunting and stabilize wildlife populations, 20 black rhinos were reintroduced into North Luangwa in 2003 (Kampamba, 2003).

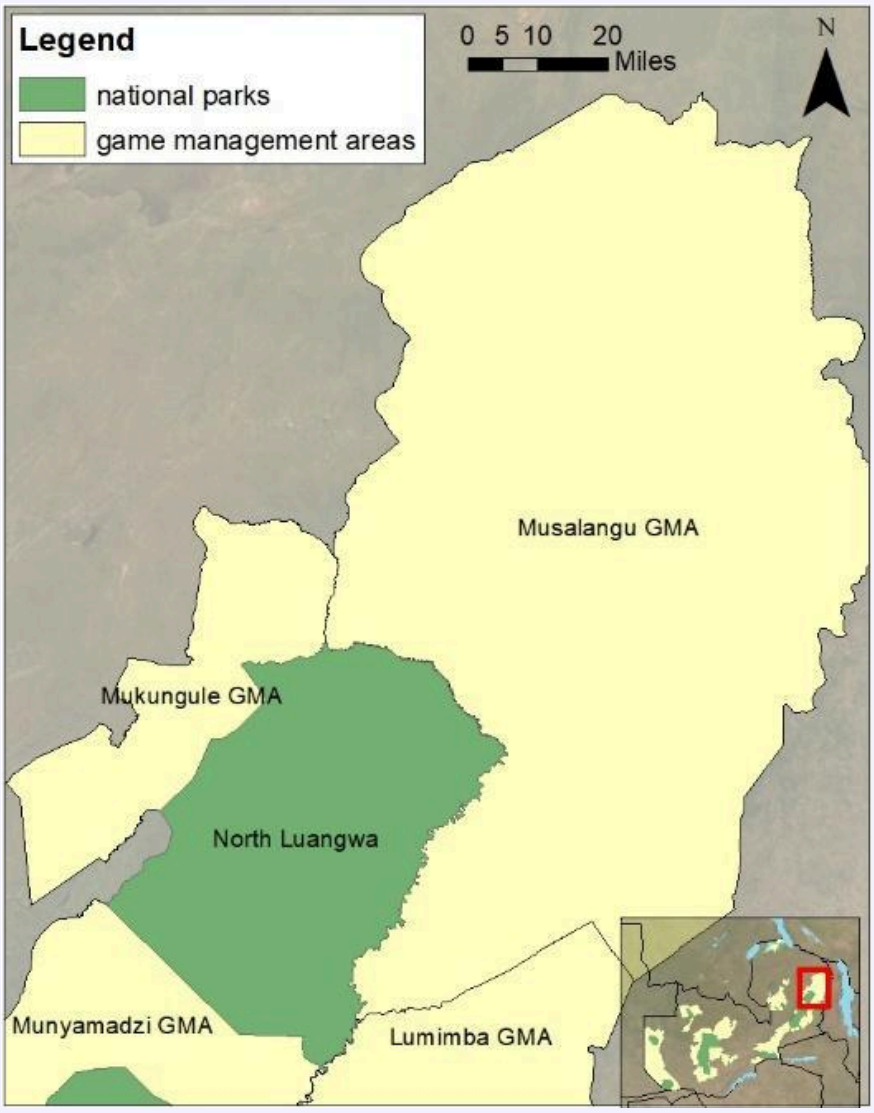

Figure 1. *Map of study region in northeast Zambia.*

Mukungule GMA (274,240 ha) is located on the western boundary of North Luangwa National Park. Most residents are ethnically Bemba and indigenous to northern Zambia. There is a community resource board made up of elected representatives from the community that make decisions on the use of natural resources and how to utilize any income or other benefits from wildlife. The GMA is subdivided into 10 village action groups that each have representatives on the community resource board.

Mukungule is currently home to one hunting concession which was responsible for 17 animals hunted by 14 clients in 2022 (Appendix S3). Communities are entitled to 50 percent of each hunting permit fee. In the past, communities have received a portion of the annual concession fee (~$36,000) and additional community fees from hunting concessions (~$11,000) annually. Frankfurt Zoological Society also supports the community directly by providing annual salaries for village game scouts ($5,500) as well as training, support, and additional projects. At least 24 community members were employed by the community resource board or the hunting outfitter.

The community has used income from wildlife to fund improvements to local school infrastructure, teacher housing, a covered market, and a hammermill, among other projects. In 2019, there were no official reports of livestock loss or crop damage in Mukungule, but data collection efforts were minimal in this region prior to 2020 (Frankfurt Zoological Society, 2023). In 2022, Mukungule residents reported the loss of 12 hectares of crops to elephants, 5 hectares to hippopotamus, and 2 hectares to primates. One person reported property damage to their home from elephants and 10 small livestock were killed by leopards in the same year. During our study period, a community member had recently been killed by an elephant while defending his field and a village game scout from a different GMA was killed by a snake bite while training in North Luangwa National Park. There are no compensation programs for human-wildlife conflict, but in 2019 Frankfurt Zoological Society began providing support for mitigation efforts such as the use of chili peppers to deter elephants from fields and construction of elephant-proof grain storage structures (Frankfurt Zoological Society, 2023).

Sampling and data collection

In June 2019, we conducted semi-structured interviews that included demographic questions, open-ended questions, free-listing, and pile-sorting. Because of our focus on human-wildlife coexistence, we sampled the three village action groups that are located closest to the park boundary where interactions with wildlife are more common. After obtaining permission from the chief of Mukungule, we approached the head of the community resource board and traditional leaders in each village to request assistance identifying participants for the study. We invited all community members from the selected villages to participate on

a voluntary basis with no tangible cost or benefit for participation. We randomly selected a subset of the volunteers. Participation was voluntary with an oral informed consent in compliance with the University of Florida's Institutional Review Board Human Subjects standards (IRB# 201801588).

The interviews took between 40 and 50 minutes to conduct. Author LM (who is conversational in Bemba) conducted all interviews with the help of one local field assistant to translate. Even if participants were fluent in English, we requested they respond in Bemba to reduce potential mistranslations. Wildlife names used in the free-listing activity were recorded in Bemba and later translated into English by several key informants (See supplementary information S1 for a complete list of wildlife names in English, Bemba, and Latin). We then verified translations using a guidebook with photos to ensure that everyone in the group agreed on the translation. Interviews were conducted privately with only the participant, researcher, and translator present.

We recorded birth year, gender, highest education level, and village for all respondents. Participants were asked about their experiences farming including whether they farm, what they grow, crop losses in the most recent growing season, and causes of these crop losses. Similarly, we asked if they own domestic animals, how many of each species, and any losses over the past year with an explanation of the loss. The free-listing and pile-sorting activities were more rigid, but to allow for the collection of additional qualitative data, we made notes of voluntary comments made during these activities. In addition, we asked follow-up questions such as why they included certain species in a category, especially if the information seemed contradictory or unusual which allowed us to ensure the activity was well-understood and accurately recorded the data we sought. These follow-up questions also provided useful qualitative information. The final semi-structured questions related to local instances of wildlife damage, what happened, when it occurred, where, and what the response was.

We used oral free-listing where participants verbally list as many examples they can think of for a given category (Newing, 2010). Participants were told that they would be asked about different types of wildlife. We intentionally used the phrase "inama sha mpanga" which translates to

"wild animals" but did not provide a definition or explanation of "wild animals." They were first asked to list all the wild animals that they like, then the wild animals that they do not like. These categories were mutually exclusive so in the few instances when a participant tried to list the same species on both lists, we asked them to choose the best list based on whether they like or dislike the animal more. Next, we asked them to free-list wild animals that cause harm or damage to humans or their livelihoods to identify species that impose actual or potential costs. Finally, we asked them to free-list wild animals that bring benefits to individuals and/or the community. These lists were not mutually exclusive as we recognize that a species can be simultaneously beneficial and harmful for different reasons. We started each interview with the free-listing activity to allow participants to determine which species were most important to them.

Lastly, we gave participants 22 laminated 3-inch by 2-inch cards with black and white drawings of individual wild animals found locally to complete a pile sorting exercise (Appendix S2). The cards included: elephant, hippopotamus, buffalo, rhinoceros, impala, kudu, crocodile, owl, bushpig, warthog, monkey, rodent, rabbit, lion, leopard, squirrel, snake, and giraffe. We asked participants to look through the cards first and identify the wild animal pictured to ensure comprehension. Then, we asked them to sort all the cards into one of two possible piles, one for animals that they would prefer to have more of in their community and one for animals they would prefer to have fewer of in the community. We used these sorted piles as a measurement of tolerance or intolerance for each of the species including those considered non-conflict species. While tolerance is highly complex, in an effort to explore relationships, we employed a simplified definition of intolerance as a preference to have fewer of a given species in their community and in contrast tolerance is a preference to have more of a given species. This activity was followed up with another sorting into two possible piles, but this time for wild animals that cause harm to humans or their livelihoods (i.e. inflict costs) and wild animals that do not cause harm.

Data analysis

We calculated summary statistics for the free-listing activities, including the proportion of participants that listed each species, the rank or position of a species on each participant's list from first to last, the average rank for each species, and the average number of species listed for each free-list.

We analyzed each species listed in each category by Smith's S, a salience score which is a combination of the number of people that listed a species and the rank of the species on each list (Smith and Borgatti, 1997). Higher Smith's S salience scores indicate species that were more prominent or important for the respective free-list category. We analyzed pile sorting results by the proportion of respondents that placed a species in each category. We inductively coded qualitative data on reasons for including wildlife on specific free-lists and confirmed the appropriateness of these categories with key informants from the community and Frankfurt Zoological Society.

We tested for correlation between liking/disliking wildlife species and expressing tolerance for them using Fisher's exact tests. While all participants classified the 22 wildlife species by tolerance, they did not all include these same species on their like or dislike free-lists. Therefore, we subset the sample by all the individuals who included these species on the dislike or like free-list and used the subset for each species to calculate Fisher's exact test. In some cases, the sample size was too small to conduct analyses on correlations.

Results

We surveyed 69 participants, of which 35 were male (51%), 46 were born in Mukungule (67%), and the vast majority engaged in agriculture and animal husbandry for their livelihoods (n= 68 farm and n= 67 own livestock). Maize is the most commonly grown crop, and the common livestock species were chicken, guinea fowl, pigeons, goats, and pigs. Most participants (n=40) experienced crop raiding in the most recent agricultural season. Of those who experienced crop damage, 22 lost crops to elephants, 16 to bushpigs, and 4 to hippopotamus. Approximately one third of participants (n=22/67) who own livestock experienced predation in the previous year with 14 people losing livestock to birds of prey, 7 to genets, 3 to leopards, and 6 to other wildlife species.

Free-listing of wildlife species

There were 41 different species included on the like lists with an average list length of 5.9 species. The dislike lists were shorter with an average of 3.3 species and 35 different species in total. Six participants declined to list wildlife that they dislike saying there were none. For harmful wildlife, there

were 21 different species listed with an average list of 4.4. Beneficial species lists included 4.2 species on average with 21 different species in total. There were 11 participants that either ended the list with “and others” or simply stated “all” despite probing to have them continue with the listing process. Follow-up questions during the free-listing activities revealed the major reasons for listing an animal in each category.

Elephant, common duiker (a small antelope) and buffalo had the highest Smith’s S salience scores (Smith’s S = 0.497, 0.491, and 0.462 respectively) for the like free-list, and these species were also listed on the dislike list by other participants. For the dislike free-lists, the species with the highest salience score was elephant (Smith’s S = 0.382) followed by bushpig (Smith’s S = 0.264) then lion (Smith’s S = 0.257) (Figure 2). Elephants had the highest salience score for beneficial (Smith’s S = 0.758) free-lists followed by rhinoceros (Smith’s S = 0.503) then buffalo (Smith’s S = 0.330). For the free-lists of harmful species, elephants had the highest salience score followed by bushpig then hippopotamus (Smith’s S = 0.882, 0.351, and 0.331 respectively) (Figure 2).

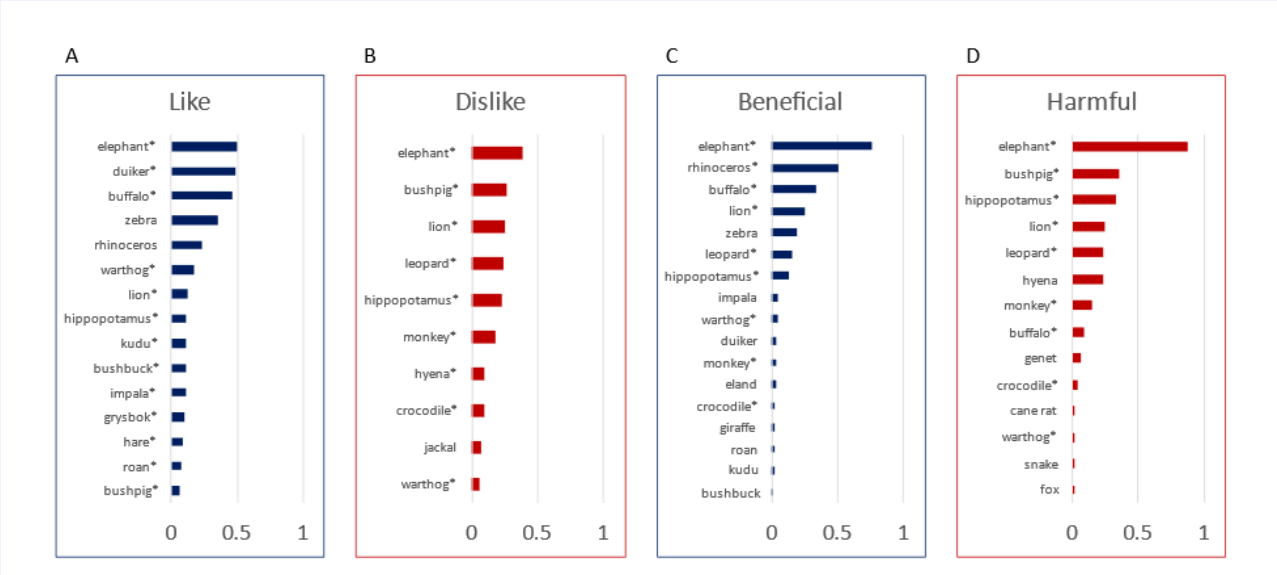

Figure 2. *Smith's S salience scores (a combination of the frequency that participants mentioned the animal in free-listing and the rank or how early in the free-listing they listed the animal) of liked (panel A), disliked (panel B), beneficial (panel C), and harmful (panel D) species with a salience score of 0.05 or higher. Asterisks denote species that were included on both like and dislike lists by different participants. Like and dislike free-lists were mutually exclusive but harmful and beneficial were not. See supplementary information S3-4 for figures of all species included on the free-lists.*

Pile sorting of wildlife species

When asked to place the 18 wildlife cards into piles of harmful and not-harmful species, there was unanimous agreement that impala and zebra were harmless while elephants were harmful. There was a strong agreement that giraffe, duiker, chameleon, kudu, and rabbit were not harmful while most participants sorted hippopotamus, snake, monkey, lion, and bushpig into the harmful pile (Figure 3).

Participants were also asked to sort the same 22 wildlife cards according to tolerance (if they are willing to have more or would prefer fewer of the species in their area). There were no unanimously tolerated or not-tolerated species. However, zebra, duiker, impala, and rabbit were the most tolerated species in that order and snake, crocodile, owl, and monkey were the least tolerated species in that order. Elephants, buffalo, lion, leopard, and hippopotamus are frequently cited for human-wildlife conflict, but were also tolerated more than expected.

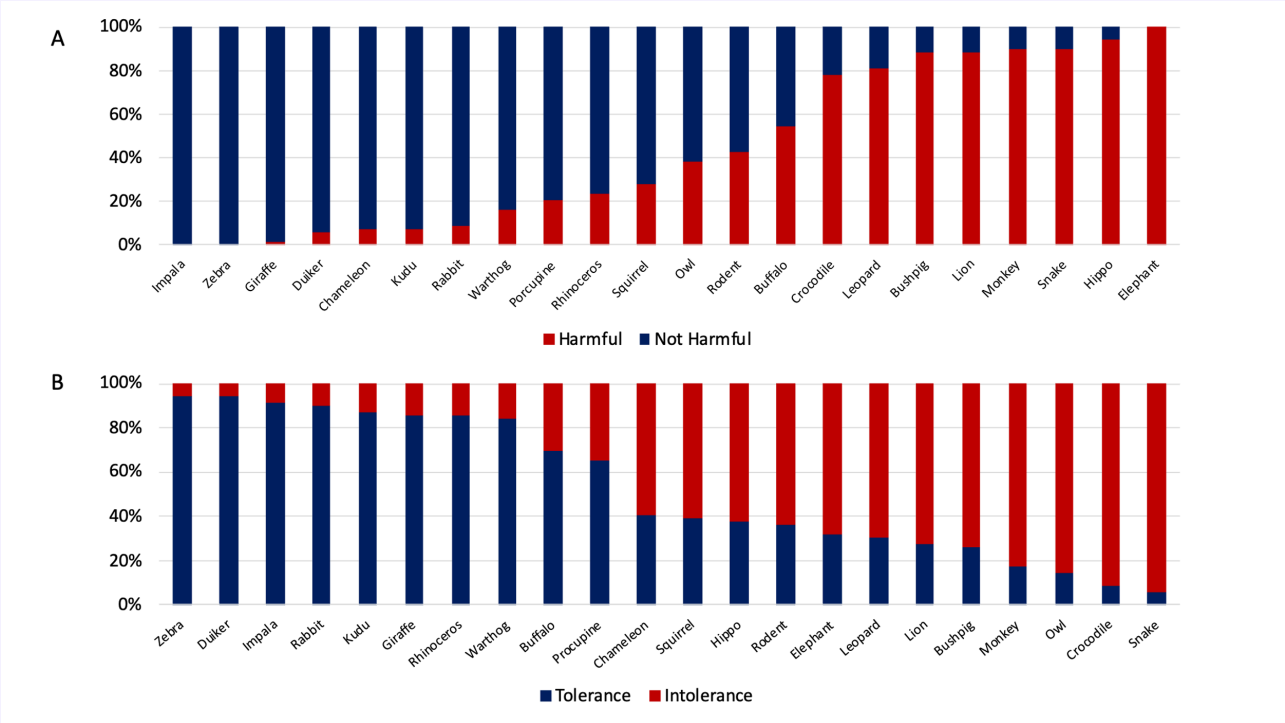

Figure 3*. Panel A shows the percentage of participants that sorted species as harmful (in red) and not harmful (in blue). Panel B shows the percentage of participants that sorted species as tolerable or those they were willing to accept more of (in blue) and those they were not tolerant of or only willing to accept fewer of (in red).*

Motivations for perceptions of wildlife species

We inductively classified reasons for liking specific wildlife into six categories: aesthetics, taste as food, potential/realized community benefits, superstitions, spiritual aspects, or family namesakes. We classified reasons for disliking specific wildlife into the following five categories: aesthetics, superstitions, spiritual aspects, personal harm/potential harm, and fear. Individuals expressed liking or disliking the way an animal looks such as an individual who said, “I do not like giraffes because their necks are too long, and they look funny” or one who said, “bushbabies’ eyes are too big, and it looks wrong.” Both these individuals acknowledged that the wildlife species (giraffes and bushbabies) are not harmful in any way nor are they linked to cultural taboos, superstitions, or religious beliefs. However, they expressed a strong dislike of the species simply because of how it looks.

Superstitions, spiritual beliefs, and cultural values were cited as reasons for liking or disliking wildlife. One participant explained how wildlife are considered part of God's creation and humans have an obligation to appreciate and look after these creatures as reflected in the Bemba phrase for natural resources (ifilengwa na Lesa) which directly translates to 'things created by God'. One person noted a superstition that if a grysbok eats from your field, it is a sign that your harvest will be bad. Multiple respondents commented on superstitions related to chameleons with some acknowledging these as beliefs while others attributed these comments to ecological knowledge. For example, one individual cited chameleons as harmful because "chameleons have a poisonous backbone and if you step on one, your foot will swell." Others explained that seeing a chameleon will bring you bad luck or illness, but that the animal itself is not physically harmful. These beliefs explain the ~7% of participants that classified chameleons as harmful in the pile sorting activity. Owls were also linked to spiritual beliefs or superstitions where their mere presence is considered a bad omen, but they were also noted for physical harm through predation of chickens and guinea fowl. Multiple participants cited cultural values and family totems or namesakes as motivations for liking animals and these cultural values may be strong enough to influence tolerance of harmful species. Most notably, multiple participants explained their motivation for liking elephants, despite their potential for crop-raiding, is because their family totem is the elephant. The only participant who listed crocodile on the liked list explained that they are a symbol of the Bemba tribe, whereas another participant explained that people can return or shift into the form of crocodiles to attack their enemies.

The explanations for classifying wildlife as beneficial were potential/realized benefits from trophy hunting, potential benefits from tourism, and meat. Multiple participants commented on how money from trophy hunting and tourism can come back to the community to help support schools or other projects. They knew which species were desirable for trophy hunting with lions, elephants, and buffalo considered the most economically beneficial. One participant declared "although elephants bring problems, they also bring benefits" while another said "they [trophy hunters] killed an elephant and we got money for our school". No participants had been employed in the wildlife sector, but many attributed

wildlife with potential for employment. They noted that income from wildlife could be used to support development like funding local schools.

When classifying species as harmful, the primary reasons were related to examples of previous harm within the community or nearby communities- crop raiding, livestock predation, or human injury/death. Respondents commented that while some wildlife species rarely come to the area, they have the potential to cause significant harm when they do come, while other species are unlikely to cause harm unless pestered. For example, a participant stated, “maybe elephants only come 2 or 3 times in a year, but they cause a lot of damage when they do [come]”. Another participant explained that “hippos are harmful, but they can not come here because we are far from the river.” Lions were another notable example as one participant said that lions rarely come to Mukungule, but can be very dangerous if they do since “they can even kill a human.” Alternatively, another participant noted “lions are not dangerous to humans, if you leave them alone, they will leave you alone”.

Correlations between liking and tolerating and wildlife related damage

Liking and tolerating were significantly correlated for elephants, hippopotamus, and buffalo at $p<0.05$ (Table 1). Because the rating for like or dislike came from free-lists, many participants did not include certain species so sample sizes were often too small to test for correlations. Twenty four percent (n=8/34) of individuals who experienced crop loss from elephants expressed tolerance for elephants while 40% (n=14/35) of individuals who had not experienced crop loss from elephants were tolerant of elephants. There was a negative linear relationship between species considered harmful and being tolerated ($p<0.001$, R-squared = 0.64) (Figure 4). As the percentage of people that considered a species harmful increased the percentage of people willing to tolerate them decreased. However, for elephants and buffalo more people were tolerant of them than expected according to the linear relationship. Conversely, fewer people were willing to tolerate chameleons or owls than expected based on the perceived harmfulness.

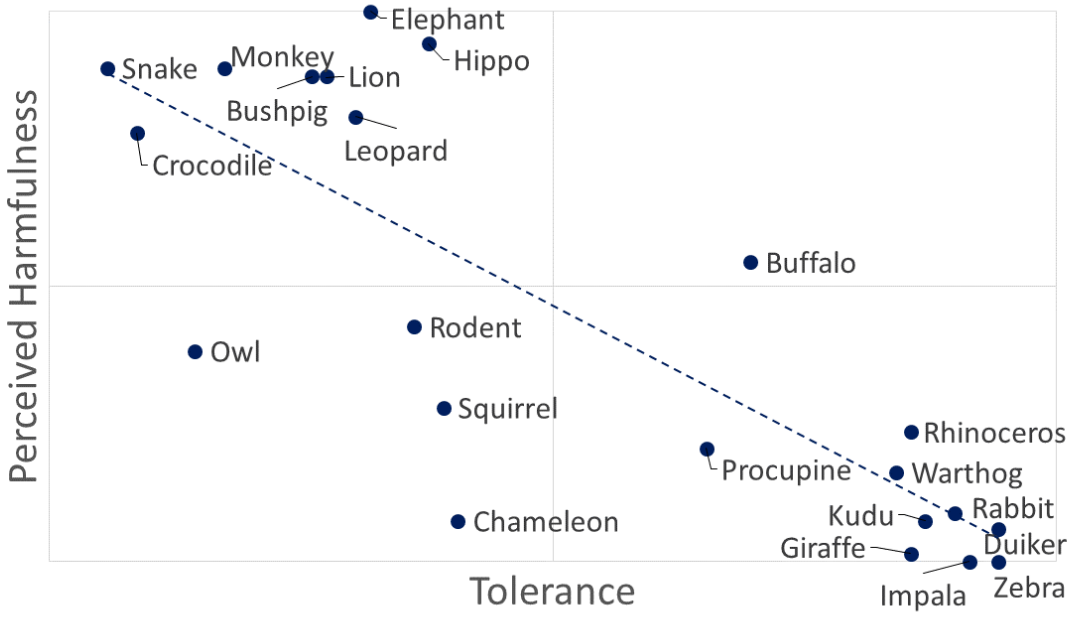

***Figure 4**. General relationship between tolerance and harmfulness of 22 wildlife species. The percentage of respondents that expressed tolerance for a species (x-axis) from low to high and the percentage of respondents that perceived the species as harmful (y-axis) from low to high with a dashed linear regression trendline.*

Discussion

We found that relationships between tolerance and attitudes, costs (harmfulness), and benefits, were complex and highly nuanced. We also found that the relative importance of different factors in determining tolerance varied across species. Attitudes were correlated with tolerance for some, but not all species. While the perceived harmfulness of a species was a significant predictor of tolerance, there were some interesting outliers.

Regarding attitudes, individuals that freely listed an animal as disliked usually classified the same animal as not tolerated, but many liked species were not classified as tolerated. While previous studies have demonstrated a strong relationship between attitudes and acceptance (e.g. Bruskotter et al., 2015), it may be more complex than previously thought. Our Fisher's

exact tests revealed a significant correlation between liking and tolerating for some, but not all species. With elephants, lions, hippopotamuses, bushpigs, leopards, crocodiles, and monkeys, 40% or more of the participants that free-listed them as liked did not have tolerance for them according to the pile sort. Instead, participants commented on liking certain wildlife, but not wanting to live with them or tolerate their presence. Therefore, efforts to improve attitudes toward wildlife species may not yield improved tolerance.

Table 1: *Comparison of number of individual participants' free-listing and pile sorting responses for like/dislike and tolerance/intolerance. All participants (n=69) classified these species based on tolerance, but the sample size for like/dislike varied based on how many participants included the species on their free-lists. Results of Fisher's exact test are displayed for cases with large enough sample sizes to test for correlation and p-values <0.05 are denoted with an asterisk.*

Species	Number who like and tolerate	Number who like and do not tolerate	Number who dislike and tolerate	Number who dislike and do not tolerate	Fisher's exact p-value
	Majority of participants mentioning species "like" the species				
Duiker	47	3	1	0	1
Zebra	40	3	0	0	
Buffalo	36	10	2	4	0.04*
Rhinoceros	23	1	0	0	
Warthog	22	1	4	2	0.1
Elephant	21	20	1	17	<0.001*
Impala	17	0	0	1	0.056
Kudu	15	0	2	0	
Rabbit	10	2	1	0	1
Giraffe	6	0	1	1	0.25
Porcupine	3	0	1	1	0.4
	Majority of participants mentioning species "dislike" the species				
Leopard	3	2	6	23	0.1
Hippo	9	8	2	22	0.003*
Lion	7	6	6	20	0.08
Monkey	4	7	3	20	0.18
Bushpig	4	5	8	20	0.43
Crocodile	1	1	1	10	0.29
Snake	0	0	0	4	
Squirrel	0	1	0	2	
Rodent	0	0	0	1	

More research is beginning to show that species tolerance does not linearly and proportionally stem from direct costs (Bencin et al., 2016; Dickman, 2010; Kansky et al., 2016). For example, researchers in the Zambezi region of Namibia found that all but one of the top four species most vulnerable to illegal hunting generated greater average annual revenue from legal hunting than average annual agricultural damage (Kahler & Gore, 2015). However, respondents in Namibia cited perceived ecological risks (e.g., disease vectors) associated with certain species, historical human fatalities, and non-equitable community conservancy benefit distribution of hunting revenues and meat shares as influencing species-based illegal killing (Kahler and Gore, 2015). Our results corroborate these findings that tolerance is not solely linked to economic value. While the majority of participants (82%) listed elephants as beneficial and many acknowledged the high potential value of elephants for trophy hunting, only 32 percent reported tolerance of elephants. Additionally, eight people who experienced crop loss in the study year still expressed a desire to live with more elephants with little to no economic benefits currently distributed. Actual costs and benefits were cited by participants as influencing attitudes and tolerance, but they were only one of many reasons.

The potential for costs or benefits, even if unrealized, was also commonly cited in reference to attitudes and tolerance. Instances of wildlife fatally attacking humans are relatively rare, but these events can be extremely traumatic (Koziarski et al., 2016). Historic deaths caused by wildlife may continue to contribute to changed attitudes and tolerance even when people rationally understand the low likelihood of being killed by a wild animal (Dickman, 2010). This is reflected in the comments of how lions are extremely harmful because they can kill humans combined with comments on the rarity of lions in the area as well as the low likelihood that a lion would attack if undisturbed. Fear was cited as a reason for disliking wildlife, which may stem from historic attacks or even unfounded beliefs/superstitions related to certain wildlife species. Prokop et al. (2009) found that hostility toward bats in Slovakia was largely driven by fear. One participant screamed when they first saw the card with an image of a snake demonstrating that severe fear of snakes can manifest even with harmless images. Reducing wildlife costs without addressing fear or perceived cost may have limited impacts on tolerance.

Participants were very knowledgeable of the potential costs and benefits of wildlife. Despite being very knowledgeable on the potential harm or benefits from wildlife, some participants disliked or were intolerant of species they recognized as harmless and potentially even beneficial. For example, only one respondent claimed that giraffes were harmful as they can eat maize, but multiple others disliked giraffes (primarily for their strange look) and one of these individuals expressed unwillingness to accept giraffes in the area despite classifying giraffes as not harmful. Alternatively, a contagious element of conflict, where conflict with one harmful species translates to reduced acceptance or tolerance of other species, may explain some of this disconnect (Dickman et al., 2014). However, there were certainly species (e.g. duiker, zebra, and rhinoceros) that were well liked and tolerated in our study. The disconnect between considering a species harmless and being willing to tolerate that species is further evidence that a simple cost or benefit analysis does not adequately explain wildlife tolerance.

While the tangible benefits received to date have been relatively small and inconsistent, there was strong agreement of the potential for wildlife to bring large amounts of money and other benefits to the community. Community based natural resource management projects in other regions of the Luangwa valley led to community benefits from trophy hunting in the 1990s, but these economic gains began declining in the 2000s (Lewis et al., 1990; Simasiku et al., 2008). Understanding of and aspirations toward potential future benefits likely influenced people's willingness to tolerate wildlife even if they personally have received few or no benefits to date. If understanding of the potential economic value of wildlife for trophy hunting was a major determinant of tolerance, then efforts to educate communities on the economic value of wildlife may impact tolerance levels even before benefits are realized. Bruskotter and Wilson (2014) found that perceived benefits were a better predictor of wildlife acceptance than perceived risk. Additionally, human-wildlife interactions are not static but rather evolve over time based on cycling of positive, negative, and neutral outcomes (Harris et al., 2023), this evolution creates a potential for diversified and seemingly contradictory perceptions related to the benefits and risks of specific wildlife species. More research is needed to explore relationships between knowledge, attitudes, and tolerance, as well as

temporal changes of tolerance in response to changes in knowledge or attitudes.

Even if a strong link between aspects of costs or benefits and tolerance are identified for a species, it can be challenging to design appropriate interventions that do not have unintended negative consequences. While increasing economic benefits may improve tolerance in the short term, in some cases it may reduce non-economic or intrinsic values of nature that are important for sustained coexistence (Lepper and Greene, 2015). Efforts to promote conflict mitigation strategies without addressing benefits can have the unintended consequence of increasing perceived risk and therefore decreasing acceptance (Bruskotter and Wilson, 2014).

An alternative hypothesis for the willingness to tolerate harmful, but potentially valuable species with little actual economic benefits to date is the devolution of wildlife rights to local communities. People are generally more willing to tolerate voluntary risks (Starr, 1969) so ownership of wildlife may result in agency needed for increased tolerance. For example, research from Mozambique showed that agreement with rules governing wildlife was a strong predictor of wildlife tolerance unlike wildlife-related costs (Merz et al., 2023). Therefore, efforts to address historical injustices and roots of conflict by transforming colonial-era wildlife management strategies to more devolved and inclusive strategies where communities help determine how to manage their local wildlife may be a vital component of successful human-wildlife coexistence. Conflicts between humans and wildlife are complex and require multifaceted approaches to their mitigation and resolution (Dickman, 2010). Examining the root causes of conflict and attempting to address those instead of the surface level conflict or direct costs from wildlife is difficult but is more likely to lead to long-term conflict mitigation and coexistence (Zimmermann et al., 2020).

The ethnoecological methods employed in this study provided a new and valuable means of uncovering the nuances of wildlife tolerance in Indigenous communities. Common attitudinal studies that use scales between harmful/beneficial or like/dislike fail to capture the nuanced attitudes and perceptions of Indigenous people and local communities who simultaneously recognize the potential benefits and costs associated with wildlife. Additionally, the free-listing exercises grant respondents the agency to determine which species are most relevant to the discussion

while semi-structured interviews promote discussion and collection of qualitative data. The pile-sorting and ranking activities allow for better comparisons between species. In developing this new application of methods to the study of tolerance we focused on links between knowledge, perceptions, and attitudes while differentiating between species. Future research is needed to address the relationships between tolerance and other factors such as behavior and to assess ownership, and governance which are seldom examined. Focus groups and other participatory methods can help better address why tolerance is so nuanced and which conservation interventions best promote human-wildlife coexistence. Conducting follow-up interviews with the same participants can shed light on the potential variability of attitudes, perceptions, acceptance, and tolerance over time to assess the influence of the immediate context. Recent events like intense instances of conflict, changes in trophy hunting income, or political advocacy to strengthen community rights are likely to impact results, but the extent of the impact cannot be assessed without long-term studies.

Conclusions

The complex and nuanced relationship between humans and wildlife poses challenges and opportunities for wildlife managers seeking to promote coexistence. Attitudes toward wildlife form from a complex mixture of experiences, values, beliefs, and personal preferences (Kansky, 2015). This complexity can make it challenging to develop conservation interventions that appropriately match the local context. However, the high level of tolerance of local people for some local wildlife in our study presents a unique opportunity to design conservation programs that build on existing attitudes and perceptions to ensure mutually beneficial coexistence.

Our results from Mukungule reveal significant nuance in peoples' perceptions and tolerance of wildlife species. There is a complex decision-making process that determines willingness to tolerate even harmful species based on a range of factors. Several participants noted the difficulty of deciding if they wanted more or fewer elephants because of the potential benefits and harm associated with them. Even the aspirations of receiving benefits or strengthening community rights in the future likely impacted peoples' perception of wildlife and willingness to tolerate certain species. Interventions designed around the assumption that tolerance

primarily stems from a simple assessment of tangible costs and benefits are unlikely to succeed in this context. We expect significant nuance in human-wildlife tolerance in other communities throughout Africa and potentially beyond, but more research is needed to explore this. Therefore, we urge conservationists to consider a wider conceptualization of how human tolerance for wildlife is determined for a given species and context. Human-wildlife coexistence outside of protected areas is ultimately determined by people's willingness to tolerate wildlife. Therefore, conservationists need to be more aware of and responsive to the motivations for human-tolerance of wildlife to design effective and acceptable conservation interventions.

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Data Availability

All data from this study are provided here.

Supplemental Information

Supplemental Information can be found here.

Transparent Peer Review

Results from the Transparent Peer Review can be found here.

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