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People and Nature

RESEARCH ARTICLE

Emotional costs and empathy are associated with tolerance towards wolves

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Abstract

1. The recovery and growing population of grey wolves (*Canis lupus*) in Germany has increased interactions with livestock owners. Ensuring the continued protection and survival of wolves requires understanding the socio-psychological factors that shape people's tolerance towards coexisting with them. While most studies focus on technical fixes, the underlying psychological and experiential drivers of human–wolf interactions remain underinvestigated. The Wildlife Tolerance Model, defined as 'the ability and inclination of an individual to absorb the extra potential or actual costs of living with wildlife', provides a framework for identifying these predictors and informing management strategies.
2. We collected data from sheep owners ($n = 42$) in northern Germany using a structured questionnaire based on the Wildlife Tolerance Model. The model included positive and negative meaningful experiences, empathy, tangible costs (e.g. livestock damage, experiences with compensation and subsidy schemes), intangible costs (e.g. negative emotions, time burden, vigilance and cognitive burden), tangible benefits (e.g. perceived monetary benefits of wolves to individuals and communities) and intangible benefits (positive emotions and non-monetary benefits of wolves to individuals, communities, humankind and nature). We applied Bayesian Structural Equation Modelling to examine relationships among these constructs and identify key predictors of tolerance.
3. Tolerance towards wolves was substantially and negatively associated with intangible costs, whereas empathy showed a substantial positive association. Positive meaningful experiences were positively associated with perceived intangible benefits, whereas the associations of negative meaningful experiences with costs and benefits were non-substantial. In contrast, tangible costs related to livestock losses showed no substantial direct association with tolerance.
4. Overall, tolerance was well explained by socio-psychological predictors, highlighting the importance of addressing worry, frustration and related emotional burdens alongside fostering empathy. These findings suggest that strategies to support coexistence should extend beyond reducing material losses and instead

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incorporate psychosocial support, empathy-building initiatives and opportunities for positive human–wolf experiences.
5. *Synthesis*. Collectively, these results highlight the value of co-adaptive management approaches that address emotional and experiential dimensions of tolerance in recolonising landscapes.

KEYWORDS
coexistence, emotions, Germany, large carnivore, socio-psychology, wildlife tolerance model

1 | INTRODUCTION

Grey wolves (*Canis lupus*) were driven to extinction in Germany during the 19th century due to persecution and extermination. However, wolves began returning to Germany from Poland, with the first reproducing pack established in 2000, after changes in the legislation (Reinhardt & Kluth, 2007). Wolves have been under special protection in the Federal Republic of Germany since 1980 (§1 BArtSchV) and throughout Germany since reunification in 1990 (Reinhardt & Kluth, 2007). Since 2000, the wolf population in Germany has grown exponentially, with an average annual increase of 36% (Reinhardt et al., 2019).

In the 2021/2022 monitoring year, 161 wolf packs, 43 wolf pairs and 21 single resident wolves were confirmed in Germany (DBBW, 2022a). As of the 2023/2024 monitoring period, the population had further grown to 209 wolf packs, 46 pairs and 19 territorial individual wolves, corresponding to approximately 1600 confirmed individuals nationwide (DBBW, 2025). The highest concentrations of wolves occur in the eastern federal states, particularly Brandenburg, Saxony and Lower Saxony. This continuing expansion highlights both the successful recolonisation of wolves in Germany and the increasing in wolf populations in multiple regions (DBBW, 2025).

Large carnivores, such as wolves, can have substantial positive effects on biodiversity and ecosystem functioning, especially through top-down trophic cascades (Sergio et al., 2008; Ripple et al., 2015). For instance, wolves can positively influence vegetation composition by reducing herbivore densities (Beschta & Ripple, 2007), highlighting the ecological significance of their return to German ecosystems. However, the territorial requirements and protein-rich diets of large carnivores can also drive them to hunt livestock or pose a direct threat to human safety (Khorozyan et al., 2015; van Eeden et al., 2018).

At the same time, large carnivores can impose substantial socio-economic rural costs on rural livelihoods, primarily through livestock predation (e.g. sheep, cattle), which represents one of the major forms of human–wildlife interaction (Khorozyan et al., 2015; Thirgood et al., 2005). These interactions can influence attitudes towards carnivores and shape management decisions, especially in regions where large carnivores are recolonising or expanding their range. For example, in Germany, where large carnivores such as bears, wolves and lynx have been extinct for such a long time, livestock farmers also have to relearn how to deal with a predator such as the wolf, as herding strategies have changed since the extinction of wolves (Reinhardt & Kluth, 2007; Schoof et al., 2021). Consistent with this, livestock predation tends to be higher than in areas where they have only recently returned than in areas where they have been continuously present (Gervasi et al., 2021). In Germany alone, 975 wolf attacks on livestock, resulting in 3374 animals killed, were documented in 2021 (DBBW, 2022b). More than 80% of the livestock killed by wolves were sheep (DBBW, 2022b).

The goal for conservationists in human–wildlife interactions, such as livestock predation by carnivores, is to foster human–wildlife coexistence. Coexistence can be understood as a dynamic and sustainable state in which humans and wildlife co-adapt to living in shared landscapes, with interactions shaped by effective institutions that ensure species persistence, social legitimacy and tolerable levels of risk (Carter & Linnell, 2016). From this perspective, coexistence is not simply the absence of adverse interactions, but an ongoing process of mutual adaptation, whereby human behaviours and management practices adapt alongside wildlife ecology to reduce negative impacts while enabling continued species persistence in multi-use landscapes. Such co-adaptation may involve changes in livestock husbandry, risk avoidance strategies and governance arrangements that foster trust, learning and dialogue among diverse stakeholder groups.

Within this framework, tolerance is a central component of coexistence. Tolerance can be conceptualised as a continuum ranging from passive acceptance to active facilitation of wildlife presence (Glikman et al., 2021). In the context of human–wolf interactions, tolerance reflects both the willingness to endure tangible costs such as livestock losses and the capacity to accommodate perceived intangible costs, including emotional and psychological responses such as worry, fear and related affective concerns (Ebrahimi-Monfared et al., 2025; Glikman et al., 2021). Understanding these socio-psychological predictors of tolerance is therefore essential for promoting coexistence, especially in regions such as northern Germany where wolves have recently recolonised and human–wolf interactions are still developing (Carter & Linnell, 2016; Glikman et al., 2021). Given the inherently human-centred nature of conservation challenges, interdisciplinary approaches that integrate ecological, social and psychological perspectives are essential for understanding and promoting coexistence (Behr et al., 2017; Dressel et al., 2015; Newing, 2011).

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Emotional responses, particularly worry about large carnivores, are increasingly recognised as important determinants of human tolerance. Worry reflects perceived threats to personal safety, livelihoods or social well-being and may shape attitudes and acceptance of carnivores even in the absence of direct negative experiences. Although worry is conceptually related to fear, it is more closely associated with anticipatory concern and sustained risk appraisal under conditions of uncertainty than with immediate responses to acute threat (Grupe & Nitschke, 2013). Empirical evidence nevertheless suggests that heightened fear can amplify perceived risk and is associated with lower tolerance towards carnivores, thereby potentially influencing coexistence outcomes (Ebrahimi-Monfared et al., 2025).

Within the broader tolerance framework, socio-psychological responses such as worry, distress and perceived risk are conceptualised as perceived intangible costs, which interact with tangible costs, including livestock losses, to shape human responses to carnivore presence (Glikman et al., 2021). Tolerance encompasses both the willingness to endure these costs and attitudes towards management, such as whether lethal control may be considered justified in specific situations or preferences for wolf population levels at different spatial scales. Coexistence with carnivores does not eliminate risk, rather, it requires humans to tolerate these risks and bring them to acceptable levels. Although managers can implement technical measures to reduce carnivore-related impacts, tolerance is often strongly influenced by social, cultural, cognitive and emotional factors, not solely by the economic or material (e.g. compensation payments) consequences of carnivore presence (Carter & Linnell, 2016). Recognising the role of these factors is therefore essential for understanding and promoting coexistence, which is particularly important in recolonising landscapes, where people are adapting to renewed interactions with large carnivores (Dickman, 2010; Ghasemi et al., 2026; Riesch et al., 2025).

Perceptions, defined as 'the way an individual observes, understands, interprets, and evaluates a referent object, action, experience, individual, policy, or outcome' (Bennett, 2016), play an important role in conservation research. Perceptions are influenced by a range of social-psychological factors such as values, norms, attitudes, beliefs, emotions or tolerance (Bruskotter & Wilson, 2014). Applying socio-psychology theories could therefore provide a more comprehensive understanding of people's affective responses towards large carnivores (Ebrahimi-Monfared et al., 2025), ultimately supporting more informed conservation and management decisions (Behr et al., 2017; Bennett, 2016; König et al., 2020). In particular, perceptions of the costs and benefits associated with wildlife have become a central focus of research on human–wildlife interactions (Bruskotter & Wilson, 2014; IUCN, 2023; Kansky et al., 2016; Thondhlana et al., 2020).

Kansky et al. (2016) proposed the Wildlife Tolerance Model as a conceptual framework linking perceptions of wildlife related costs and benefits to people's tolerance towards wildlife, including large carnivores. Tolerance is defined as 'the ability and willingness of an individual to absorb the additional potential or actual costs associated with coexisting with wildlife' (Carter & Linnell, 2016; Kansky et al., 2016). The model proposes that positive and negative meaningful experiences constitute the initial antecedents that form perceptions of wildlife-related costs and benefits, which in turn influence tolerance (Kansky et al., 2016).

These experiences influence perceptions of tangible and intangible costs and benefits (Kansky et al., 2016). Tangible costs are direct costs incurred from living alongside wolves, such as monetary losses caused by livestock predation. Intangible costs comprise non-monetary socio-psychological burdens, including distress, fear, worry and other opportunity costs resulting from direct and indirect interactions with wildlife.

Tangible benefits refer to monetary gains for individuals or communities, such as compensation payments, subsidies for mitigating measures or income generated through wolf-related tourism. Intangible benefits encompass positive emotions and non-monetary values associated with wolves, including their significance to individuals, communities, humanity and nature (Kansky et al., 2016; Marino et al., 2021). Collectively, these perceived costs and benefits are proposed to predict tolerance. In addition, the model includes other social-psychological factors, such as empathy (e.g. the ability to feel compassion when imagining a wolf) and perceptions of institutional performance (e.g. skills and knowledge in wolf management), which may also influence tolerance (Kansky et al., 2016; Marino et al., 2021).

Marino et al. (2021) applied the Wildlife Tolerance Model to examine landowners' tolerance towards grey wolves and brown bears around two protected areas in central Italy. They identified that perceived intangible costs and perceived intangible benefits were consistently associated with tolerance, whereas negative meaningful events were indirectly influencing tolerance. Although the relative importance of these drivers varied between the two regions, examining tolerance towards wolves in northern Germany provides an opportunity to evaluate the wildlife tolerance model under a different social and ecological context (Kansky et al., 2024).

The wolf population in Germany is expected to grow (Kramer-Schadt et al., 2020), and farmers' attitudes have been shown to become more negative as wolf populations increase (Eriksson et al., 2015). Consequently, fostering coexistence is likely to require adaptive strategies that evolve over time, highlighting the importance of understanding the factors that are associated with human tolerance. Tolerance towards large carnivores among livestock farmers is shaped not only by tangible factors, such as monetary losses resulting from livestock predation, but also by socio-psychological factors, including perceived intangible costs, empathy and other emotional responses (Ebrahimi-Monfared et al., 2025; Moures-Nouri et al., 2023). Therefore, understanding how socio-economic and socio-psychological factors interact to shape tolerance is essential for managing human–carnivore interactions and promoting coexistence. Given that sheep owners are among the stakeholder groups most affected by wolf recolonisation in Germany, identifying the key associations of their tolerance towards wolves may help inform future coexistence strategies.

Here, we aimed to evaluate how socio-economic and socio-psychological factors shape sheep owners' perceptions of and tolerance towards wolves in northern Germany. Guided by the Wildlife Tolerance Model, we tested the following four hypotheses:

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1. Positive and negative meaningful events with wolves would be associated with sheep owners' perceptions of intangible costs, intangible benefits and tangible costs, which would in turn influence their tolerance.
2. Intangible costs, intangible benefits and empathy would mediate the relationship between positive and negative meaningful events and tolerance towards wolves. Tangible costs were expected to be negatively associated with tolerance.
3. Empathy towards wolves would be positively associated with sheep owners' tolerance.
4. Positive and negative meaningful events might also be associated with tolerance, although these relationships were expected to be weaker than those operating indirectly through perceived costs and benefits.

2 | MATERIALS AND METHODS

2.1 | Study area

Our study area was conducted in the Lüneburger Heide natural region of the federal state of Lower Saxony, encompassing seven counties in northeastern Germany (blue lines, Figure 1). A pilot study was conducted in three additional counties in Lower Saxony and across the entire federal state of Brandenburg (yellow lines, Figure 1). These areas support high wolf densities and were therefore considered key regions for studying human–wolf coexistence (Figure 1).

2.2 | Study design

We designed structured questionnaires and created online surveys using the software LimeSurvey (Schmitz & LimeSurvey Team, 2006–2023). The study population comprised sheep owners residing within the study area. Since this group was not easily accessible, we relied on the snowball sampling approach. In addition, the Lower Saxony Sheep Breeding association (Landdesschafzuchtverband Niedersachsen e.V) disseminated the questionnaire through its website and a newsletter sent to all members. Following this, initial participants were identified through publicly available online contact information were approached, and additional associations and authorities were contacted to forward the questionnaire to sheep owners. The questionnaire consisted of demographic information of the participants as well as hypothesised variables related to wildlife tolerance model. These questions were based on the questionnaire used (or tested) in a study on landowners' tolerance towards

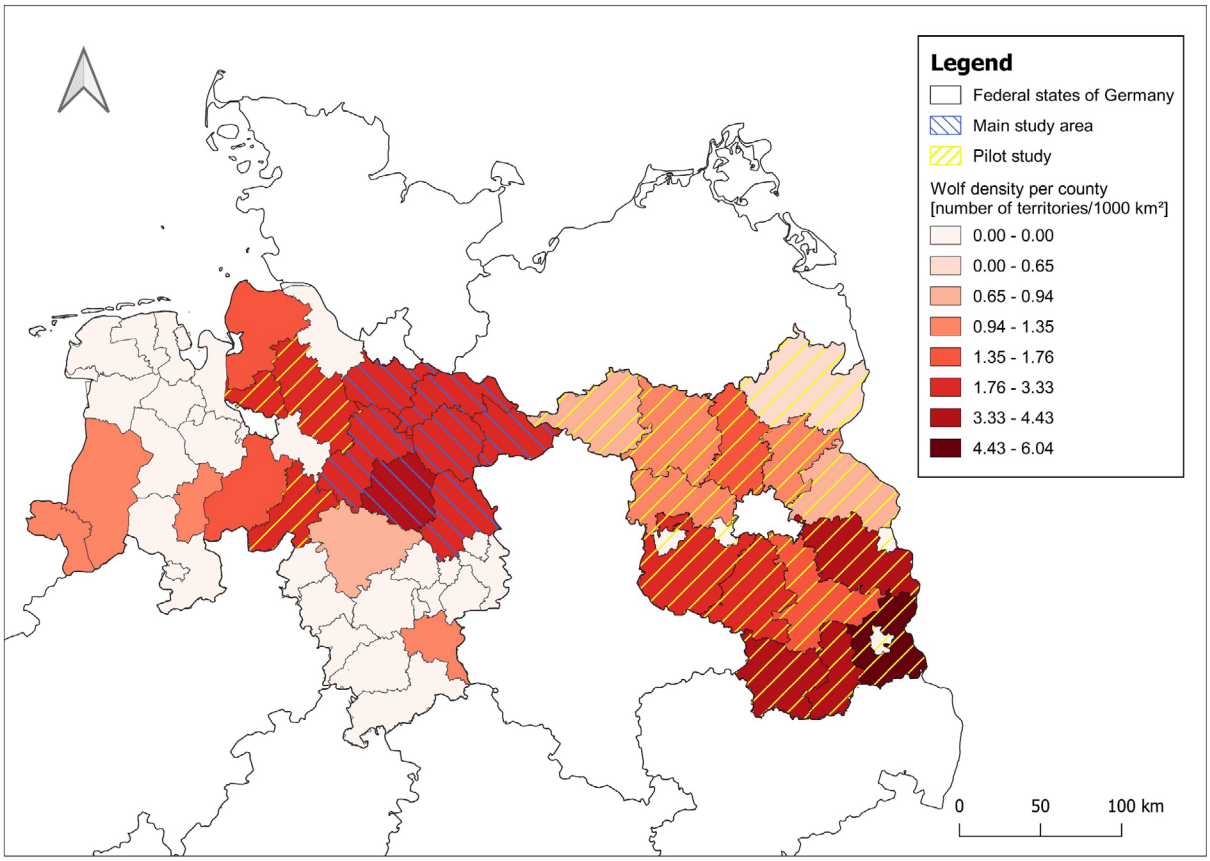


FIGURE 1 The federal states of Lower Saxony and Brandenburg with the wolf density per county calculated as the number of territories (2021/2022) per 1000 km^2. Wolf territory data from Landesjägerschaft Niedersachsen e. V. (2023) and DBBW (2022a). The main study area consisting of seven counties in the federal state of Lower Saxony (blue lines) and the piloting and additional study area consisting of three more counties in the federal state of Lower Saxony and the whole federal state of Brandenburg (yellow lines).

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wolves and bears in Italy by Marino et al. (2021) (Tables S1–S4). Our hypothesised constructs were guided based on Kansky et al. (2016) (Table S1). The pilot study and the main study were conducted between September 2023 and March 2024 (see details in Supporting Information).

2.3 | Ethical approval

The questionnaire survey for this study was conducted online through a created website. A consent letter was provided to respondents in the online questionnaire, clearly stating that their participation was entirely voluntary and that they could stop answering the questionnaire at any time. This study received ethical approval retrospectively (May 2026) from the ethics committee of Georg-August-Universität Göttingen, in accordance with institutional and national research guidelines.

2.4 | Wildlife tolerance model

The Wildlife Tolerance Model was proposed by Kansky et al. (2016), which includes several latent constructs: Positive Meaningful Events (PME), Exposure (EXPO), Negative Meaningful Events (NME), Intangible Benefits (IB), Tangible Benefits (TB), Intangible Costs (IC), Tangible Costs (TC), Institutions (INS), Empathy (EMP) and Tolerance (TOL) (Tables S1–S4). Each construct was measured through questionnaire items (Tables S2–S4).

2.5 | Statistical analyses

We applied Bayesian structural equation modelling (SEM) to examine the relationships among these constructs and identify their observed indicators specified in the Wildlife Tolerance Model (Figure 2). Bayesian SEM simultaneously estimates the measurement and structural components of the model, which allows both direct and indirect relationships to be evaluated while explicitly accounting for measurement uncertainty, making it particularly suitable for small sample sizes (Muthén & Asparouhov, 2012). Latent constructs, such as intangible benefits and tolerance, were measured indirectly using multiple observed indicators.

2.5.1 | Bayesian SEM specifications

We conducted a two-step Bayesian SEM procedure:

Step 1. Measurement model:

Observed indicators y were linked to latent variables η as follows:

$$y = \nu + \Lambda\eta + \varepsilon, \varepsilon \sim \text{Normal}\,(0, \Theta),$$

where y and $(\eta_1, \ldots \eta_p)^T$ denote the observed indicators and the vector of latent constructs, respectively, comprising the latent constructs

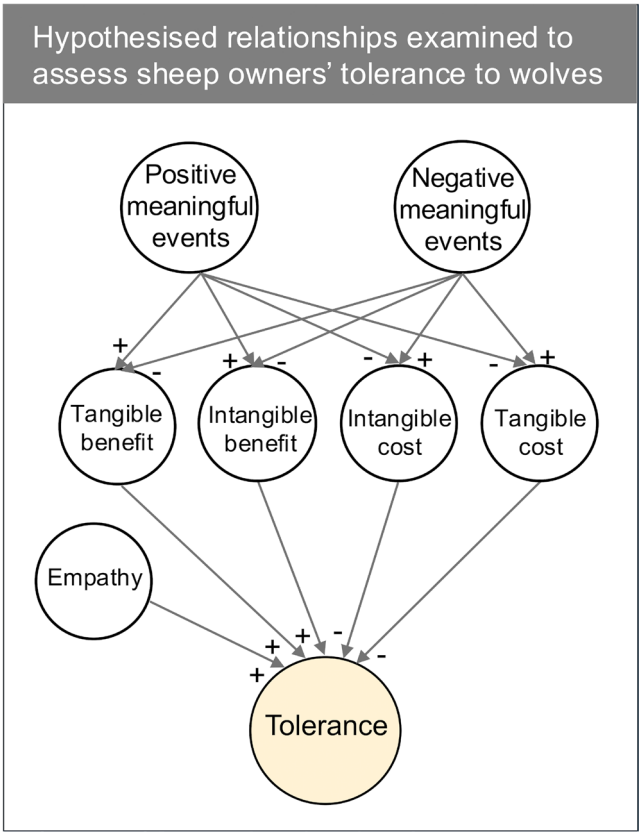


FIGURE 2 The diagram shows the hypothesised relationships among the constructs of the Wildlife Tolerance Model used to assess sheep owners' tolerance towards wolves in northern Germany. The lines represent hypothesised effects, with positive (+) and negative (−) signs indicating expected directions.

included in each candidate model (intangible benefits, tangible benefits, intangible costs, empathy and tolerance). We selected weakly informative normal priors to the estimated (free) factor loadings ($\lambda_{ij} \sim$ Normal (0, 0.01)) where the second parameter denotes precision. We assigned weakly informative Gamma priors to the residual precision parameters ($\tau \sim$ Gamma (1, 1)) and a Wishart prior to the latent precision matrix (Gelman et al., 2013; Merkle & Rosseel, 2018; Muthén & Asparouhov, 2012).

Step 2. Structural model:

In this step, we specified relationships among the latent variables and the exogenous predictors $x \in R^3$ (i.e. positive meaningful events, negative meaningful events and perceived tangible costs) as:

$$\eta = \alpha + B\eta + \Gamma x + \zeta, \quad \zeta \sim \text{Normal}\,(0, \Psi).$$

Intangible benefits and intangible costs were regressed on the exogenous predictors, positive meaningful events and negative meaningful events, whereas tolerance was regressed on intangible benefits, intangible costs, empathy and perceived tangible costs (Figure 2). We assigned weakly informative normal priors to the structural coefficients (β, $\gamma \sim$ Normal (0, 0.01)), and weakly informative Gamma priors were assigned to the latent residual precision

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parameters ($\tau \sim$ Gamma (1, 1)) to stabilise estimation while avoiding strong prior influence (Gelman et al., 2013; Merkle & Rosseel, 2018; Muthén & Asparouhov, 2012).

2.5.2 | Model fitting

Prior to model fitting, we assessed collinearity among the observed and latent variables using Spearman's rank correlation coefficients. We then fitted four-candidate SEMs, comprising three theory-driven and one exploratory model (Model-4), that differed in their inclusion of latent variables and structural paths. Models were implemented in JAGS (Just Another Gibbs Sampler) (Plummer, 2003) using jagsUI package (Kellner, 2024) in R version 4.5.3 (R Core Team, 2025) and following the Bayesian SEM framework described by Merkle and Rosseel (2018) and general Bayesian modelling practices described by Kéry and Schaub (2012). Models were estimated using Markov Chain Monte Carlo (MCMC) sampling. For each model, three MCMC chains were run with 75,000 burn-in iterations and 150,000 sampling iterations, applying thinning every five iterations (thin = 5). We specified SEM's directional relationships based on the Wildlife Tolerance Model. However, since our data were observational, we interpret these relationships as associations rather than evidence of causality and use non-causal language when describing our findings.

2.5.3 | Model comparison and selection

We compared the four-candidate Bayesian SEMs using leave-one-out cross-validation (LOO) which evaluates predictive performance while accounting for model complexity (Vehtari et al., 2017). Candidate models represented progressively simplified versions of the Wildlife Tolerance Model, developed to retain the original theoretical framework as closely as possible while reducing model complexity to accommodate the relatively small sample size ($n = 39$) (Vehtari et al., 2017). The final model selection was based on predictive performance, convergence diagnostics, posterior predictive model fit and the extent to which the resulting model remained theoretically consistent and substantively interpretable. The model-4 was conducted as an exploratory extension of the Wildlife Tolerance Model rather than a replacement of its original theoretical structure.

2.5.4 | Model validity and performance

We evaluated the validity and performance of the best-fitting Bayesian SEM model using a set of complementary Bayesian diagnostics. Overall, we assessed model fit primarily using posterior predictive *p*-values (PPP), which compare the discrepancy between the observed data and datasets replicated from the posterior predictive distribution. The PPP represents the proportion of posterior samples for which the replicated discrepancy exceeds the observed discrepancy, with values closer to 0.5 indicating better agreement between the model and the observed data, whereas values approaching 0 indicate evidence of model misfit (Merkle & Rosseel, 2018; Muthén & Asparouhov, 2012).

We also assessed convergence using Gelman–Rubin potential scale reduction factor (Rhat) and visual inspection of trace plots, with values close to 1 indicating adequate convergence and mixing across chains (Merkle & Rosseel, 2018; Muthén & Asparouhov, 2012). We evaluated the credibility of structural parameter estimates using 95% credible intervals (CrI), interpreting associations as substantial when intervals clearly excluded zero, less substantial when they narrowly excluded zero and uncertain when they included zero (Benjamin et al., 2018). We assessed the internal consistency of latent constructs by calculating composite reliability (ω) from standardised factor loadings and residual variances. Finally, we quantified explanatory power using Bayesian R^2 for endogenous constructs, representing the proportion of variance explained by the structural model (Gelman et al., 2019).

3 | RESULTS

Overall, we received 42 completed online surveys, of which 39 respondents were included in the analysis. Three surveys were excluded because they had more than 15% missing values. We removed items with more than 5% missing data, including all three items related to the exposure construct. However, items positive meaningful events (pme_1) and negative meaningful events (nme_1), pertaining to the single-item constructs, were retained despite having slightly more than 5% missing data (5.13%) (Table S2).

3.1 | Participants' characteristics

Of the 39 questionnaires analysed, 27 respondents were male, 11 were female, and one was identified as gender diverse. Most respondents (48.7%) were aged between 50 and 69 years. Sheep farming was the main source of income for only 35.9% of respondents, and the majority (58.9%) reported earning less than 10,000 Euros per year from it. Most respondents (59.0%) owned more than 100 sheep, whereas only 12.9% owned fewer than 25. All respondents used at least temporary fencing for their sheep, with 97.4% employing electric fencing and 20.5% using non-electric fencing. Fladry was used by 7.7% of respondents. A substantial proportion also utilised working dogs for sheep management. 64.1% used herding dogs, and 23.1% used livestock guarding dogs (Supporting Information). A substantial proportion also used working dogs for sheep management. Overall, 64.1% used herding dogs and 23.1% used livestock guarding dogs (see Table S5). Descriptive statistics for the observed tolerance indicators included in the SEM (Table S6).

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3.2 | Statistical results

3.2.1 | Relationships among latent variables and indicators

Our post-hoc analysis revealed that the strongest positive association was between Intangible Benefits and Tolerance ($\rho = 0.67$), while Intangible Benefits and Intangible Costs showed the strongest negative association ($\rho = -0.76$, Table S7). At the indicator level, Spearman's correlations within each latent construct were all above 0.47 (Figure 3), indicating that the indicators consistently measured their respective constructs. These results supported the specification of the latent variables in the subsequent Bayesian structural equation models.

3.2.2 | Results of model relationships

The measurement model showed adequate fit to the observed data (PPP = 0.798). All retained indicators had positive factor loadings (λ), with the 95% credible intervals excluding zero (Table S8), indicating that the latent constructs were reliably measured by their respective observed indicators. In the structural model, positive meaningful events were positively and substantially associated with intangible benefits ($\beta = 0.32$, 95% CrI = 0.04–0.62), whereas negative meaningful events showed a weak and non-substantial negative association with intangible benefits ($\beta = -0.14$, 95% CrI = −0.42 to 0.13) (Figure 4; Table S9). Moreover, positive meaningful events were weakly negatively associated with intangible costs, with the 95% credible interval only marginally excluding zero ($\beta = -0.28$, 95% CrI = −0.58 to −0.00), whereas negative meaningful events showed a minimal, non-substantial positive association

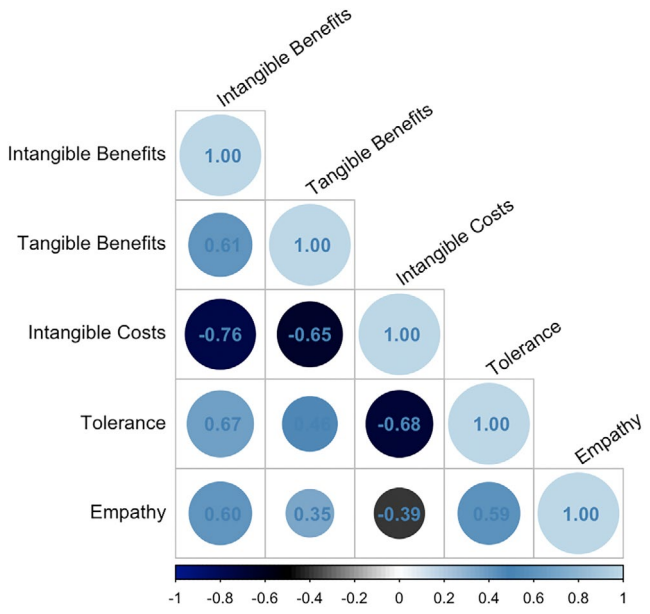


FIGURE 3 Spearman's rank correlation coefficients among latent variables.

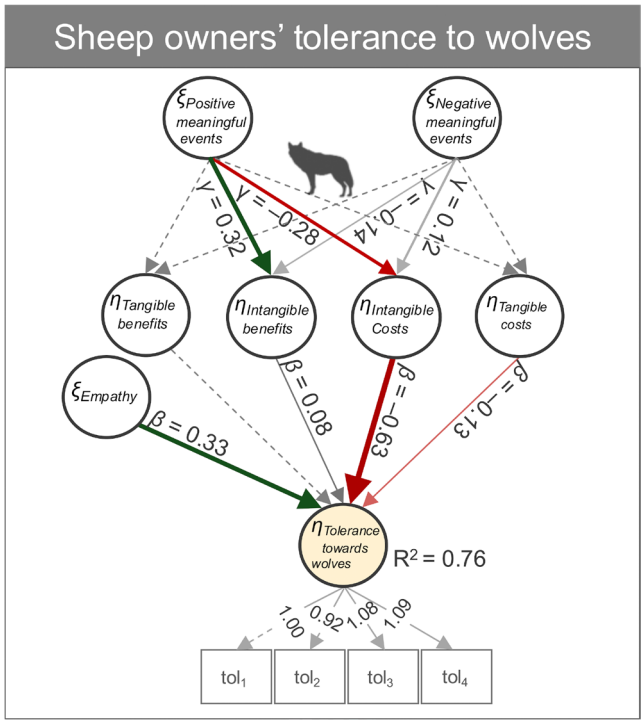


FIGURE 4 Results of the best-fitting Bayesian structural equation modelling (SEM) examining sheep owners' tolerance towards wolves in northern Germany. Values on the arrows are the posterior mean estimates for the latent regressions (gamma γ) and structural regression (beta β). The grey lines connecting latent construct tolerance (TOL) to its indicators (tol1-tol4) indicate the factor loadings (λ). Arrow colour indicates the direction and strength of the estimated relationships. Green arrows show positive effects, and red arrows represent negative effects, with thicker arrows indicating larger coefficient magnitudes. Light red arrows indicate marginal negative effects, where the 95% CrI only slightly overlaps zero. Grey arrows indicate non-substantial effects, where the 95% CrI includes zero. Dashed arrows represent relationships that were not evaluated in the candidate model set.

with intangible costs ($\beta = 0.12$, 95% CrI = −0.15 to 0.41) (Figure 4; Table S9). Tolerance was negatively associated with intangible costs ($\beta = -0.63$, 95% CrI = −1.11 to −0.21) and substantially positively associated with empathy ($\beta = 0.33$, 95% CrI = 0.06–0.61). In contrast, intangible benefits ($\beta = 0.08$, 95% CrI = −0.36 to 0.52) and tangible costs (number of sheep killed or injured by wolves between 2021 and end of June 2023; $\beta = -0.13$, 95% CrI = −0.33 to 0.07) showed weak associations with tolerance (Figure 4; Table S9).

3.2.3 | Model validity

1. Model comparison based on leave-one-out cross-validation (LOO-CV) identified model-2 as the best-performing candidate model (Tables S9 and S10). The best-fitting Bayesian SEM model showed good overall fit, with a posterior predictive *p*-value

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of PPP = 0.792 (Figures S1–S3) and a Bayesian root mean square error of approximation (BRMSEA) of 0.072 (95% CrI = 0.00–0.54). Markov chain Monte Carlo diagnostics indicated satisfactory convergence and mixing for all estimated parameters ($\hat{R} = 1.00$) (Figures S1–S6). Composite reliability (ω) was high for all latent constructs, ranging from 0.83 for intangible benefits (IB) to 0.94 for tolerance (TOL) (Table S11). Bayesian R^2 values indicated that the latent regressions explained 52% of the variance in IB and 51% in intangible costs (IC), while the structural model explained 76% in tolerance (TOL). Collectively, our results reveal good reliability, convergence, predictive performance and explanatory power of the final best-fitting model.

4 | DISCUSSION

Our findings revealed that 76% of the variation in respondent's tolerance towards wolves was explained by the variables included in the model. In our study region, wolves were extinct and have only recolonised the region over the past three decades. Studies have shown that the longer people coexist with wolves, the more negative their attitudes and acceptance of wolves tend to became (Dressel et al., 2015; Eriksson et al., 2015). This shift is often associated with increasing direct experience, perceived risks to safety or livelihoods and local exposure to wolf populations, highlighting the importance of assessing how tolerance changes over time (Eriksson et al., 2015). Our findings further showed that perceived intangible costs and empathy were associated with people's tolerance towards wolves. Future studies are needed to determine whether reducing intangible costs or fostering empathy can increase tolerance and promote coexistence with wolves.

5 | EXPERIENCES

We found that meaningful events, emotionally charged experiences with wolves that have occurred during an individual's lifetime, influenced tolerance through indirect effects (Kansky et al., 2016). Both positive and negative meaningful events were indirectly associated with tolerance through intangible costs. A similar pattern was reported by Marino et al. (2021) for negative meaningful events in two independent regions (PNALM & RMGAG) and for positive meaningful events in one of their studied regions (RMGAG). In addition, Marino et al. (2021) showed that, in regions with long-established wolf populations (PNALM), positive and negative meaningful events influenced tolerance both directly and indirectly through intangible benefits. They also highlighted that addressing landholders' concerns before encounters with wolves or bears can reduce the negative effects of these experiences, particularly fear and worry, when information is framed to resonate with the target audience.

In our study area, positive meaningful events were positively associated with intangible benefits, whereas negative meaningful events showed the opposite pattern by decreasing intangible benefits and increasing intangible costs. However, only intangible costs were substantially associated with tolerance, whereas the association between intangible benefits and tolerance was weak. These findings suggest that meaningful experiences primarily influenced tolerance through their effects on perceived intangible costs rather than perceived intangible benefits. Therefore, positive experiences alone may not be sufficient to increase tolerance among sheep owners directly affected by wolves. This highlights the importance of additional factors, such as empathy, education or targeted risk mitigation, to promote coexistence.

An increase in positive meaningful events may be associated with higher tolerance through their associations with intangible benefits and, more importantly, lower intangible costs. However, these relationships are likely to vary across stakeholder groups. For example, Arbieu et al. (2020) found that, in Germany, many members of the general public perceived encounters with wolves as positive, whether these encounters occurred in the wild or in captivity. In contrast, for landowners and livestock owners, encounters are often associated with perceived risks to livelihoods. Accordingly, while wildlife parks with wolves or guided wolf observation excursions may serve as effective tools to promote positive meaningful events among the general public, their association with tolerance among livestock owners may be more limited and context dependent. Reducing negative meaningful events may similarly contribute to higher tolerance towards wolves. Livestock owners and hunters report more negative experiences than the general population in Germany (Arbieu et al., 2020), presumably because they are more likely to experience negative interactions with wolves, such as livestock predation (Jacobs et al., 2012). Reducing such negative experiences is therefore important, and protective measures can play a key role. For instance, electric fencing and electric fladry have shown promising results, and the use of livestock guarding dogs (Soofi et al., 2022) or temporary physical deterrents is also recommended to protect livestock from wolves (Bruns et al., 2020). Subsidies for some of these measures are available in place in Brandenburg and Lower Saxony (LWK Niedersachsen, 2022a; MLUK Brandenburg, 2022). However, protection measures cannot fully prevent livestock predation events, and their effectiveness may vary over time and among livestock owners (Khorozyan & Waltert, 2019). These interventions should therefore be adapted to specific stakeholder groups, recognising that uptake and outcomes differ according to individual circumstances, experience with wolves and available resources. Thus, further research on the long-term effectiveness of protection measures is warranted to continue to reduce negative experiences for livestock owners.

Marino et al. (2021) found that exposure was negatively associated with tolerance towards wolves in one of the two regions (PNALM), although this factor was excluded from our analysis due to missing values. In PNALM, greater exposure was associated with higher tangible and intangible costs and lower intangible benefits, whereas no substantial associations with exposure were found in RMGAG. Across Wildlife Tolerance Model case studies, exposure was a significant predictor in approximately 50% of the cases (Kansky et al., 2014). While reducing lower exposure, for example, through making human

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properties less attractive to wolves, may be associated with fewer negative experiences, its association with tolerance is likely to vary among individuals and contexts.

5.1 | Benefits

Distinguishing between intangible and tangible benefits is important in understanding wildlife tolerance, as highlighted by Kansky and Knight (2014). Intangible benefits comprise non-monetary benefits, such as positive emotions related to living with wildlife or cultural values. However, we did not find a substantial association between intangible benefits and tolerance. In contrast, Marino et al. (2021) reported a substantial positive relationship between intangible benefits and landowners' tolerance towards wolves in two regions in Italy. Other studies applying the Wildlife Tolerance Model have similarly found that intangible benefits were substantially associated with tolerance in approximately 90% of case studies (Kansky et al., 2014). Although our best-fitting model did not identify a substantial association between intangible benefits and tolerance, this construct should not be disregarded in human–wildlife coexistence research.

Tangible benefits such as monetary subsidies for livestock protection measures (e.g. LWK Niedersachsen, 2022b; MLUK Brandenburg, 2022), were excluded from the best-fitting model as they neither improved model fit nor meaningfully explained variation in tolerance in our study area. This suggests that, at least in northern Germany, financial incentives may be less important in shaping sheep owners' tolerance towards wolves. This aligns with other findings, where tangible benefits showed a non-substantial association with tolerance in many case studies involving wildlife species (Kansky et al., 2014).

Although both intangible and tangible benefits did not appear as key predictors in our model, previous research suggests that intangible benefits may still play a more important role than monetary benefits in fostering tolerance. Interventions that promote positive perceptions, such as non-violent communication programmes highlighting the non-monetary advantages of wildlife may therefore support coexistence (Kansky et al., 2024; Kansky & Maassarani, 2022). In addition, previous research suggests that tangible benefits may indirectly contribute to tolerance by enhancing intrinsic motivation or valuation, a process referred to as the motivation crowding effect (Kansky et al., 2014, 2020). For example, sharing revenue from wolf tourism with local livestock owners may indirectly increase tolerance.

5.2 | Costs

Intangible costs in our study refer to non-monetary psychological costs such as distress and irritation and worry, as well as opportunity costs. While worry is conceptually related to fear, it reflects anticipatory concern and ongoing vigilance rather than immediate fear responses (Borkovec et al., 1983; Grupe & Nitschke, 2013). In our questionnaire, we measured worry, furious and irritated emotions rather than fear per se, and our results indicate that intangible costs were substantially associated with lower tolerance. This highlights the strong association between these psychological burdens and sheep owners' tolerance towards wolves in northern Germany.

Similar findings have been reported in Italy, where intangible costs were negatively associated with tolerance towards wolves in both study regions, though the effects were somewhat weaker than those observed here (Marino et al., 2021). Previous studies also emphasise the centrality of intangible costs in human–wildlife interactions, with Kansky and Knight (2014) identifying them as the most important predictor of attitudes and other studies highlighting the need for further research (Dechner, 2020; Jacobsen et al., 2021; Manoa et al., 2020; Redpath et al., 2013).

Addressing intangible costs should therefore be a primary focus of efforts to promote tolerance. While educational interventions and information campaigns are commonly suggested (Johansson et al., 2016), these alone are unlikely to alleviate the distress of livestock owners who face the real risk of wolf predation. Programmes that provide psychosocial support or structured engagement with the emotional burden of coexisting with wolves may be more promising, though additional research is needed to evaluate their effectiveness.

In contrast, tangible costs such as monetary losses due to livestock predation or time spent on mitigation measures did not have a substantial effect on tolerance in our study. Although compensation schemes exist in the study region (LWK Niedersachsen, 2022b; MLUK Brandenburg, 2024) and may partially offset losses, these payments often fall below the breeding value of livestock (Faß, 2018). Other studies also indicate that tangible costs may be less influential for tolerance once compensation mechanisms are in place (Kansky et al., 2016). Therefore, in our context, intangible costs appear more important than tangible costs and should be prioritised when developing strategies to foster tolerance towards wolves.

5.3 | Empathy

Empathy reflects the capacity to take the perspective of wolves to consider their needs alongside human concerns. Our results indicate that empathy showed a substantial positive association with sheep owners' tolerance towards wolves, suggesting that those with greater empathy towards wolves tend to report greater tolerance towards them (Marino et al., 2021). This finding is consistent with previous wildlife tolerance model studies, in which empathy was often strongly associated with tolerance (Kansky et al., 2014, 2016, 2021). From a co-adaptive coexistence perspective, fostering empathy may support adaptive human–wildlife interactions, where both human behaviours and management strategies evolve alongside ecological conditions (Carter & Linnell, 2016). Although interventions targeting empathy remain relatively rare, evidence suggests that it can be nurtured through educational and training programmes (Feshbach & Feshbach, 2011). For instance, non-violent communication training programmes have

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shown promise in enhancing perspective-taking and promoting more positive attitudes and behaviours towards wildlife (Kansky & Maassarani, 2022; Rosenberg & Chopra, 2015; Williams et al., 2021). Such approaches could be integrated into management strategies aimed at increasing tolerance among sheep owners.

A recent interdisciplinary review highlights that effective management of human–carnivore interactions requires attention to cultural, social, psychological (Ebrahimi-Monfared et al., 2025) and historical contexts, rather than a sole focus on technical solutions (Pooley et al., 2023). Neglecting these dimensions, including perceived intangible costs, local perceptions and social norms can limit the effectiveness of interventions aimed at improving tolerance (Riesch et al., 2025). Our results indicate that empathy was associated with sheep owners' tolerance towards wolves, aligning with experimental evidence that empathy towards nature and humans can promote conservation-oriented behaviours (Raymond et al., 2025). Future research should investigate whether interventions that foster empathy, alongside socio-cultural, psychological and educational approaches, can increase tolerance and promote coexistence with wolves.

5.4 | Caveat

Our study has three limitations. First, the sample size ($n = 39$) was relatively small. However, Bayesian SEM (Merkle & Rosseel, 2018) is well suited for small samples because it estimates full posterior distributions and does not rely on large-sample approximations (Muthén & Asparouhov, 2012; van de Schoot et al., 2015). Nevertheless, the relatively small sample size warrants cautious interpretation of the findings and replication in larger populations.

Second, some items and constructs were removed during model selection. The initial model included all hypothesised constructs; however, based on model ranking, factor loadings, Bayesian R^2 and composite reliability, the best-fitting model retained only the most informative variables. Notably, recent exposure to wolves was excluded, which means its association with tolerance could not be assessed.

Third, some constructs were represented by few indicators. For example, tangible costs were ultimately represented by a single observed variable, namely the number of sheep killed or injured by wolves over a 2.5-year period. Although single-item constructs can reduce predictive validity for latent perceptions (Diamantopoulos et al., 2012), this variable shows an observable and quantitative measure, making its inclusion appropriate. Despite these limitations, the best-fitting model showed good convergence, satisfactory posterior predictive fit and high explanatory power, providing support for the robustness and consistency of the estimated relationships within the proposed model.

6 | CONCLUSION

We conclude that identifying the drivers of sheep owners' tolerance towards wolves is important for informing efforts to improve dialogue and reduce negative interactions between livestock farmers and conservationists in Germany. The Wildlife Tolerance Model provides a practical, reliable and comparable theoretical framework for identifying these drivers. Our results offer insights that can help to inform management decisions aimed at improving tolerance within a co-adaptive coexistence context, in which management strategies and human responses may evolve over time alongside changing ecological conditions (Carter & Linnell, 2016).

Our findings indicate that intangible costs and empathy were the primary predictors of sheep owners' tolerance towards wolves. In this research, intangible costs were captured through emotional responses such as worry, distress, frustration and irritation associated with living with wolves. While these emotions are closely related to fear, our results support interpreting their effects primarily in terms of sustained worry and anticipatory concern rather than acute fear responses (Ebrahimi-Monfared et al., 2025). Consequently, management efforts may benefit from addressing these forms of intangible costs as part of an adaptive process of learning and adjustment, for example through psychosocial support or dialogue-based approaches for affected livestock owners. In addition, empathy showed a positive direct association with tolerance, suggesting that initiatives aimed at fostering perspective-taking towards wolves could be explored as a means of supporting more tolerant attitudes. However, further research is needed to evaluate the uptake and effectiveness of such initiatives across different social groups. Furthermore, positive and negative meaningful events were indirectly associated with tolerance through their associations with intangible costs and intangible benefits, highlighting the role of lived experiences in shaping tolerance. This suggests that management strategies that seek to reduce negative meaningful events (e.g. through effective livestock protection) and cautiously promote positive experiences with wolves may complement existing approaches. Overall, our findings suggest that management interventions that extend beyond tangible costs and attend to the emotional and experiential dimensions of tolerance may help inform efforts to support coexistence in landscapes shared with large carnivores.

AUTHOR CONTRIBUTIONS

Annika Metz conceived the study, collected the data, designed the methodology, conducted the initial analyses and prepared the initial draft of the manuscript. Mahmood Soofi led the study during the revision process, conducted the statistical analyses, handled the revisions and wrote and revised the manuscript. Matthias Waltert contributed to manuscript editing. All authors critically revised the manuscript and approved the final version for publication.

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CONFLICT OF INTEREST STATEMENT

The authors do not have a conflict of interest.

DATA AVAILABILITY STATEMENT

To avoid sharing potentially identifiable data, only the anonymised data used in the analyses and the R code are publicly available on Zenodo (Metz et al., 2026): https://doi.org/10.5281/zenodo.22729931.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Description of the Wildlife Tolerance Model constructs (latent variables) used to assess sheep owners' tolerance towards wolves in northern Germany. The constructs are based on the Wildlife Tolerance Model framework described by Kansky et al. (2016).

Table S2. The questions and indicators that were used to define the variables of the Wildlife Tolerance Model, which were tested in this study. The scale and calculation of the indicator score are also reported.

Table S3. Questions used to calculate the item tc_3: Number of mitigation measures used.

Table S4. Questions about the demographic information of participants.

Table S5. Demographic characteristics of participants and mitigation measures used by sheep owners ($N = 39$).

Table S6. Descriptive statistics for the observed indicators of the latent tolerance construct included in the structural equation model.

Table S7. Indicator-level Spearman correlations (ρ) and corresponding p-values between indicators of latent constructs in the Wildlife Tolerance Model (WTM) for sheep owners in northern Germany.

Table S8. Standardised posterior factor loadings for the Bayesian measurement model. Posterior means, standard deviations (SD) and 95% credible intervals (CrI) are shown for the observed indicators of each latent construct.

Table S9. Posterior summaries for the best-fitting (selected based on LOO) Bayesian structural equation model fitted in JAGS. The table reports factor loadings (λ), latent regressions (γ) and structural regressions (β) for Model 2, with posterior means, SDs and 95% credible intervals.

Table S10. Summary of the ranking and performance of four Bayesian structural equation models fitted in JAGS to examine sheep owners' tolerance towards wolves in northern Germany. All models were based on the Wildlife Tolerance Model proposed by Kansky et al. (2016). Models were ranked using leave-one-out cross-validation (LOO), summarised by the expected log pointwise predictive density (elpd-LOO), the leave-one-out information criterion (LOOIC) and Δelpd-LOO. Models 1–3 represented theory-driven simplifications of the original Wildlife Tolerance Model, whereas Model 4 was an exploratory model that combined Intangible Benefits and Intangible Costs into a single Evaluation (EV) construct. Model fit was assessed using posterior predictive p-values (PPP) and the Bayesian root mean square error of approximation (BRMSEA). Higher elpd-LOO (less negative values) and lower LOOIC indicate better predictive performance, whereas Δelpd-LOO = 0 identifies the highest-ranked model.

Table S11. McDonald's composite reliability (ω) and Bayesian coefficient of determination (R^2) for the latent constructs across the four Bayesian structural equation models fitted in JAGS. McDonald's ω was calculated from the posterior distributions of factor loadings and residual variances and reflects the internal consistency of each latent construct. Bayesian R^2 represents the posterior mean

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proportion of variance explained for endogenous latent variables.

Figure S1. Trace plots of the Markov chain Monte Carlo (MCMC) samples for the structural regression parameters in the final Bayesian structural equation model (Model 2) fitted in JAGS. The plots illustrate chain mixing and convergence for the regression coefficients that are linked to Positive Meaningful Events (PME) and Negative Meaningful Events (NME) to Intangible Benefits (IB) and Intangible Costs (IC), and the coefficients associating to Tangible Costs (TC), Intangible Benefits (IB), Intangible Costs (IC) and Empathy (EM) to Tolerance (TOL).

Figure S2. Posterior predictive check for best fitting (Model 2). The grey density area shows the posterior predictive distribution of the discrepancy statistic, and the red line indicates the observed discrepancy. The posterior predictive *p*-value (PPP = 0.792) supports an adequate model fit.

Figure S3. Posterior predictive discrepancy plot for the best-fitting model (Model 2). The grey density shows the posterior predictive distribution of the discrepancy statistic, and the red line indicates the observed discrepancy (PPP = 0.792).

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