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Beneficial Spillover Effects of Antipredation Interventions Support Human–Carnivore Coexistence

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ABSTRACT

Reducing human–wildlife conflict is critical for global biodiversity conservation and supporting livelihoods in landscapes where people and wildlife co-occur. Interventions intended to reduce conflicts and their negative outcomes are diverse and widespread, yet there is often a dearth of empirical evidence regarding effectiveness, particularly at appropriate spatiotemporal scales. We investigate an underappreciated question relevant to large carnivore–livestock systems globally regarding spillover effects of anti-conflict interventions: Do fortified livestock enclosures modify carnivore predation on livestock for neighbors who lack such interventions? We use ca. 25,000 monthly reports from agropastoralists in an East African landscape critical for large carnivore conservation. Results from Bayesian multilevel statistical models demonstrate robust effects of fortified livestock enclosures in reducing reported predation not only in target households, but also in neighboring households that lack such fortification—a beneficial spillover effect. Results provide empirical evidence for policy and practice regarding tools to reduce large carnivore conflicts while pointing to the important role of complex-systems processes in determining coexistence outcomes.

1 | Introduction

Coexistence among people and wildlife is inhibited by significant conflict. Wildlife predation on crops and livestock can negatively impact the health and well-being of farmers and livestock owners (Naughton-Treves 1998; Thirgood et al. 2005; Barua et al. 2013; Salerno et al. 2016; Braczkowski et al. 2023). Such conflicts can, directly and indirectly, shape human behaviors that harm wildlife, from retaliatory killing to support for policies allowing lethal control or eradication, which impacts coexistence potential across landscapes (Dickman 2010; Van Eeden, et al. 2018; Carter and Linnell 2023). For large carnivores, conflicts with people pose significant threats to populations globally, potentially undermining their important role in ecosystems (Ripple et al. 2014).

Notable scientific attention has been recently directed toward conceptualizing human–wildlife coexistence generally (Carter and Linnell 2016; König et al. 2020; Pooley et al. 2021) and specifically regarding carnivores (Oriol-Cotterill et al. 2015; Beck et al. 2019; Venumière-Lefebvre et al. 2022). Likewise, substantial management and husbandry efforts are directed toward minimizing predation on livestock, including lethal control of carnivores and non-lethal antipredation strategies like night-penning of livestock, guarding dogs, and various deterrents (e.g., fladry, strobes) (Van Eeden, et al. 2018; Lorand et al. 2022). Such strategies, alongside facilitative social norms, are seen as necessary to support human tolerance of carnivores (Treves and Bruskotter 2014). However, we often lack robust, site-specific evidence on the effectiveness of antipredation strategies (Van Eeden, et al. 2018; Khorozyan 2022; Lorand et al. 2022). Prominent among uncertainties is how these strategies affect the interactions of people, livestock, and carnivores in shared landscapes across space and time, potentially through feedback and other complex-systems processes such as spillovers (Carter et al. 2014).

Here, we focus on spillover effects as one such underappreciated interaction that may impact the effectiveness of antipredation strategies and overall coexistence. For our purposes, we define beneficial spillovers as the effects of an in situ intervention to reduce the probability of predation at larger scales (e.g., across a neighborhood or landscape) by conferring a protective effect on people and livestock where the intervention is absent. We define detrimental spillovers as the effects of an intervention to reduce the probability of predation at the site of implementation but to displace an increased risk to neighbors (e.g., Musiani et al. 2003; Lesilau et al. 2018). Consistent with the general lack of empirical evidence regarding antipredation strategies, few studies have explicitly examined spatial or temporal spillover effects in human–wildlife conflict systems (Santiago-Avila et al. 2018; Carter et al. 2020), and the presence of beneficial spillovers is largely undocumented.

Because little is known about spillover effects, their role in shaping both intended and unintended outcomes is unclear, which has significant implications when managing for coexistence. For instance, the adoption of bear-proof trash cans by residents may reduce returns on foraging in residential neighborhoods, thereby limiting human–bear conflicts locally, but impacts in adjacent urban and peri-urban areas for both humans and bears are less clear (Johnson et al. 2020). If such spillover effects were known—as when the lethal removal of an apex predator in response to predation on livestock increases overall losses from mesopredators in the surrounding landscape (Elbroch and Treves 2023)—intervention design and modification would be more cost-effective and avoid unintended systems-level outcomes.

We investigate spillover effects from an important antipredation intervention—fortified livestock enclosures. We used a unique longitudinal dataset: ca. 25,000 monthly reports of livestock losses from households in one of the most important large carnivore strongholds globally, the Ruaha-Rungwa Landscape (RRL) of southern Tanzania. RRL comprises core-protected wildlife habitat surrounded by extractive reserves and community-managed conservation lands. Predation on livestock on community lands by lions (*Panthera leo*), leopards (*Panthera pardus*), and hyenas (*Hyaena* spp.) is common and significantly impacts agropastoralist livelihoods; these lands also play an important role in increasing effective core wildlife habitat if conflict can be effectively managed. Our findings aim to provide robust empirical evidence for policy and practice regarding spillover effects and tools to reduce conflicts while contributing more broadly to the science of human–wildlife coexistence.

2 | Methods

Human–carnivore conflicts, along with conservation efforts to promote coexistence, are ongoing across communities adjacent to Ruaha National Park (ca. 20,000 km^2) and within the broader RRL (ca. 45,000 km^2), which protects important populations of lion, leopard, hyena, African wild dog (*Lycaon pictus*), and cheetah (*Acinonyx jabutus*) (Strampelli et al. 2023). Fortified livestock enclosures—1.8-m-high chain-link fenced corrals, or night pens, constructed to replace traditional acacia thorn enclosures—have been adopted by some households living adjacent to MBOMIPA Community Wildlife Management Area (Figure 1; Grau et al. 2025). These pastoralist and agropastoralist households, predominantly from Sukuma, Maasai, and Barabaig ethnic groups, graze livestock in the surrounding landscape during the day and use night pens, either traditional acacia thorn enclosures or wire-fenced fortified enclosures. Households typically use fortified enclosures to protect only some vulnerable livestock at night, while other livestock remain in the household compound or adjacent traditional enclosures (Grau et al. 2025).

Prior evidence shows that fortified enclosures are effective at reducing predation on livestock, yet they have been adopted by a minority of households in the landscape (Grau et al. 2025; also, Weise et al. 2018; Kissui et al. 2019). Construction costs, though subsidized, are a barrier, while larger-scale adoption is likely shaped by multiple factors such as perceived effectiveness, social acceptability, and political context (Dickman 2010; Boronyak et al. 2020). High rates of nocturnal predation persist in households utilizing only traditional enclosures (Grau et al. 2025); most households experience some predation during daytime grazing (Abade et al. 2014a).

2.1 | Predation and Enclosure Data

Since 2009, a conservation organization, Lion Landscapes (LL), has worked to reduce carnivore conflicts by subsidizing the costs of fortified enclosures. LL conducts monthly monitoring of both fortified- and traditional-enclosure households, tracking self-reported livestock ownership and loss due to disease, theft, and predation. In 2019, records became spatially explicit, permitting examination of spatiotemporal spillover effects of fortified enclosures on traditional-enclosure neighbors. Data used to investigate spillover effects include 24,975 monthly reports from 630 households. When data collection began in 2019, 115 fortified-enclosure households existed; when data collection concluded in 2023, 251 fortified-enclosure households existed (Figure 2). A total of 482

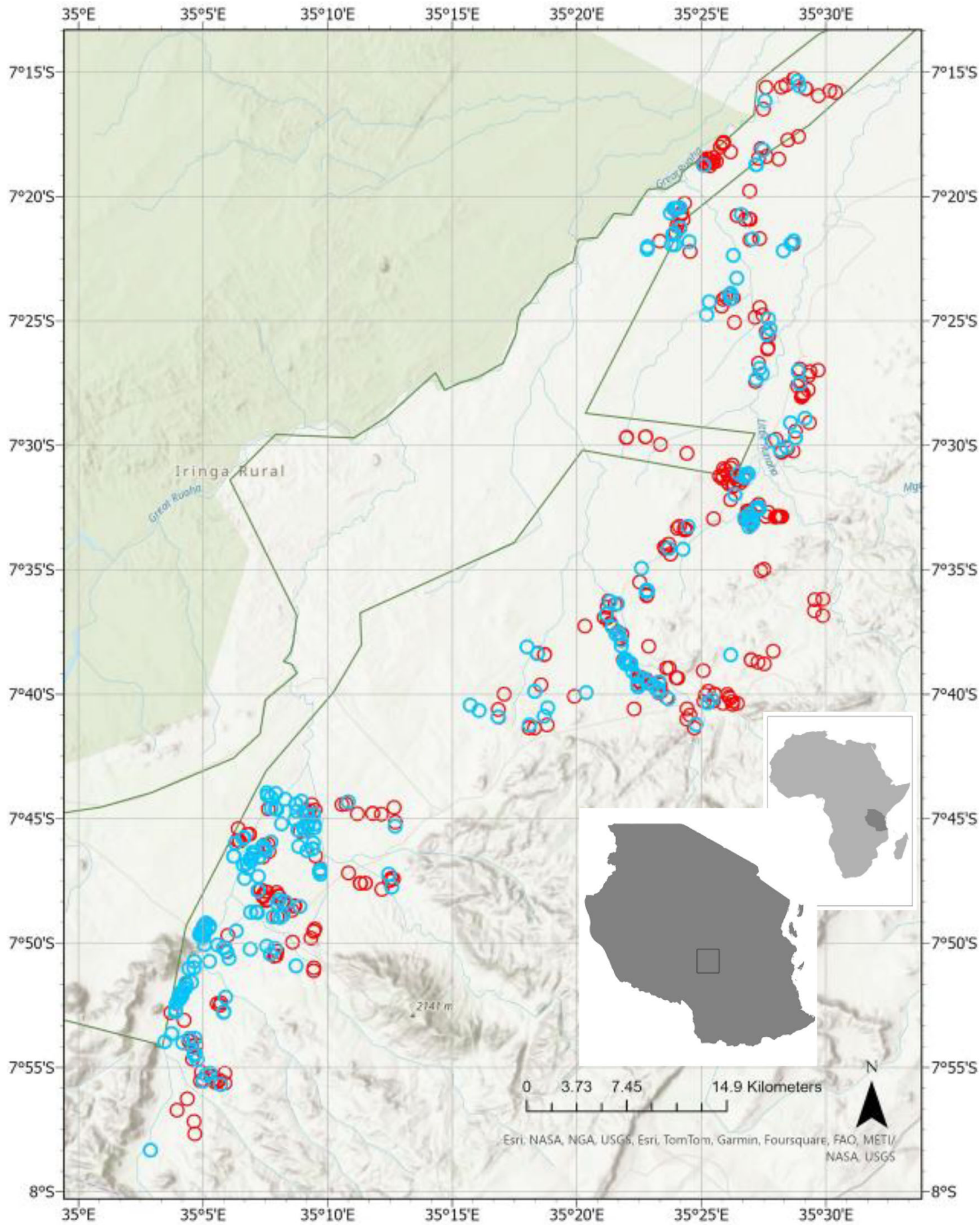

FIGURE 1 | Study system in the Ruaha-Rungwa Landscape, Tanzania. Data are drawn from agropastoralist households providing monthly reports of carnivore predation on livestock, 2019–2023. Points represent locations of households on community lands with traditional (red circles) and fortified livestock enclosures (blue circles) as of December 2022. MBOMIPA Community Wildlife Management Area (green boundary) buffers Ruaha National Park (solid green); human settlement and land use intensity tends to increase with distance from these boundaries.

households were unfortified (i.e., traditional) during all or part of the monthly record. Such time series are required to estimate the effectiveness of conflict interventions using observational data (Denninger Snyder et al. 2023). Households did not always report to local monitors; on average, 67% of households in the sample reported each month. However, efforts to maintain systematic monitoring across households were in place, thereby limiting the likelihood of bias in overreporting or underreporting of predation events.

Since predation on livestock was extremely infrequent in fortified-enclosure households (Grau et al. 2025), and because our core questions regarding spillover effects are about impacts on traditional-enclosure households, we fitted models (described

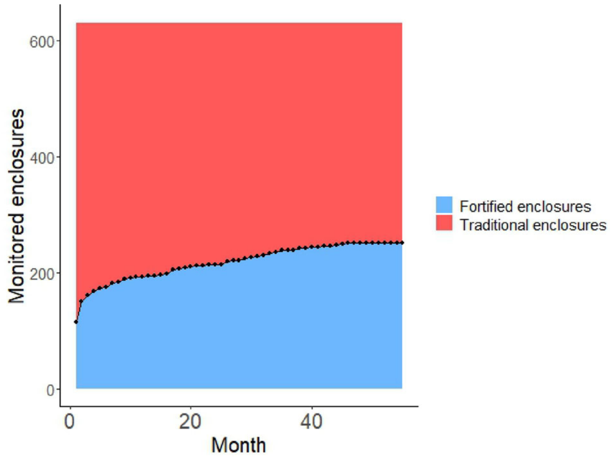

FIGURE 2 | Proportion of fortified and traditional enclosures, April 2019 to December 2023. Data used in the analyses were drawn from 630 households. Fortified enclosures increased from 115 to 251 over the study period. Models estimating spillover effects are fitted to data from the 482 households that had traditional enclosures for all or part of the study period.

below) to data from only the 15,988 monthly reports from traditional-enclosure households.

We created two covariates to capture spillover effects (either beneficial or detrimental), each calculated monthly. First, we estimated kernel density surfaces using the {SpatialKDE} package in R (Caha 2023), which aggregated the influence of individual fortified enclosures across the local neighborhood (Figure 3). Second, we calculated the linear distance between each traditional-enclosure household and its nearest fortified-enclosure neighbor. The two approaches account for our uncertainty regarding how spillover effects may be conferred, allowing for distinct spatial relationships of aggregate effects (via kernel density) or the effect of only the nearest neighbor (via linear distance) to be estimated.

2.2 | Analyses

We test for the presence and direction of spillover effects using Bayesian multilevel binomial logistic regression. Our outcome is Bernoulli distributed—the occurrence of a reported livestock depredation event in a traditional-enclosure household (1/0) at each household-month. As repeat sampling occurred across households and months, we estimated varying intercepts (i.e., hierarchical, random, or mixed effects) for each household and month. A Bayesian approach using regularized priors and a non-centered parameterization of the variance–covariance matrix with a Cholesky transformation permits thorough mixing and reliable estimation of parameters, especially when empirical probabilities are low (McElreath 2020).

Our binary response variable encoded whether in each survey month, t, a traditional-enclosure household, i, reported predation. For our purposes, we define a predation event as the household reporting losses to a carnivore of one or more cattle, sheep, and/or goats. The species of carnivore was not reported due to known difficulty with verification (Grau et al. 2025). The main model included five fixed-effect covariates: (1) kernel density value from fortified enclosures corresponding to household i, and (2) its quadratic term (see Figure 3); (3) linear distance between household i and its nearest fortified-enclosure neighbor, and (4) its quadratic term; and (5) linear distance between household i and the boundary of Ruaha National Park as a control covariate because proximity to the park is associated with increased predation (Dickman et al. 2014). The quadratic terms on both kernel density and nearest neighbor covariates account for nonlinear effects or the probability of predation to intensify or diminish with magnitude. While the inclusion of data on carnivore presence in the models would afford expanded inference, such data are unavailable. Abade et al. (2014b) model carnivore presence from camera trap data primarily in Ruaha National Park, with few observations drawn from community lands in our study, and predicted surfaces are uninformative in those areas.

We fitted an additional model that permitted exploration of temporal spillover effects specifically from newly constructed fortified enclosures, such as might be predicted if carnivores exhibit neophobia (Crane and Ferrari 2017). We created additional monthly kernel density surfaces from only those fortified enclosures constructed during the data record; pre-existing fortified enclosures were omitted. For these new surfaces, we used months since fortification as a weight parameter. The resulting covariate captures the mean age of newly constructed fortified enclosures in the neighborhood of each traditional-enclosure household, i. This secondary model includes only time since construction as a fixed effect, along with varying intercept effects for households and months. Both models used standardized predictor covariates.

We estimated models using a Hamiltonian Monte Carlo process in CmdStanR, called through R (Gabry and Češnovar 2023). We adapted code and fitted models using the ulam() command from the {rethinking} package (McElreath 2020). Results present coefficient estimates as joint-posterior means with 95% credible intervals, which represent the range of values within which the coefficient is likely to fall, given the data, model, and priors. See Supporting Information for details on data, models, and diagnostics.

3 | Results

Data reveal appreciable impacts of carnivores on people through predation on livestock. Over the study period, on average, ca. 3% of traditional-enclosure households reported predation each month. A total of 846 predation events were reported in traditional-enclosure households, while the number of households with fortified enclosures increased from 115 to 251 (Figure 2). Notably, reported livestock losses were far greater to disease (5192 total) than to predation by carnivores.

We fitted statistical models to data from the 482 traditional-enclosure households that were unfortified for all or part of the study period. Model estimates show evidence of beneficial spillover effects from fortified enclosures on their traditional-enclosure neighbors. Predation probability increases for traditional-enclosure households as the distance to the nearest fortified enclosure increases, but eventually levels off

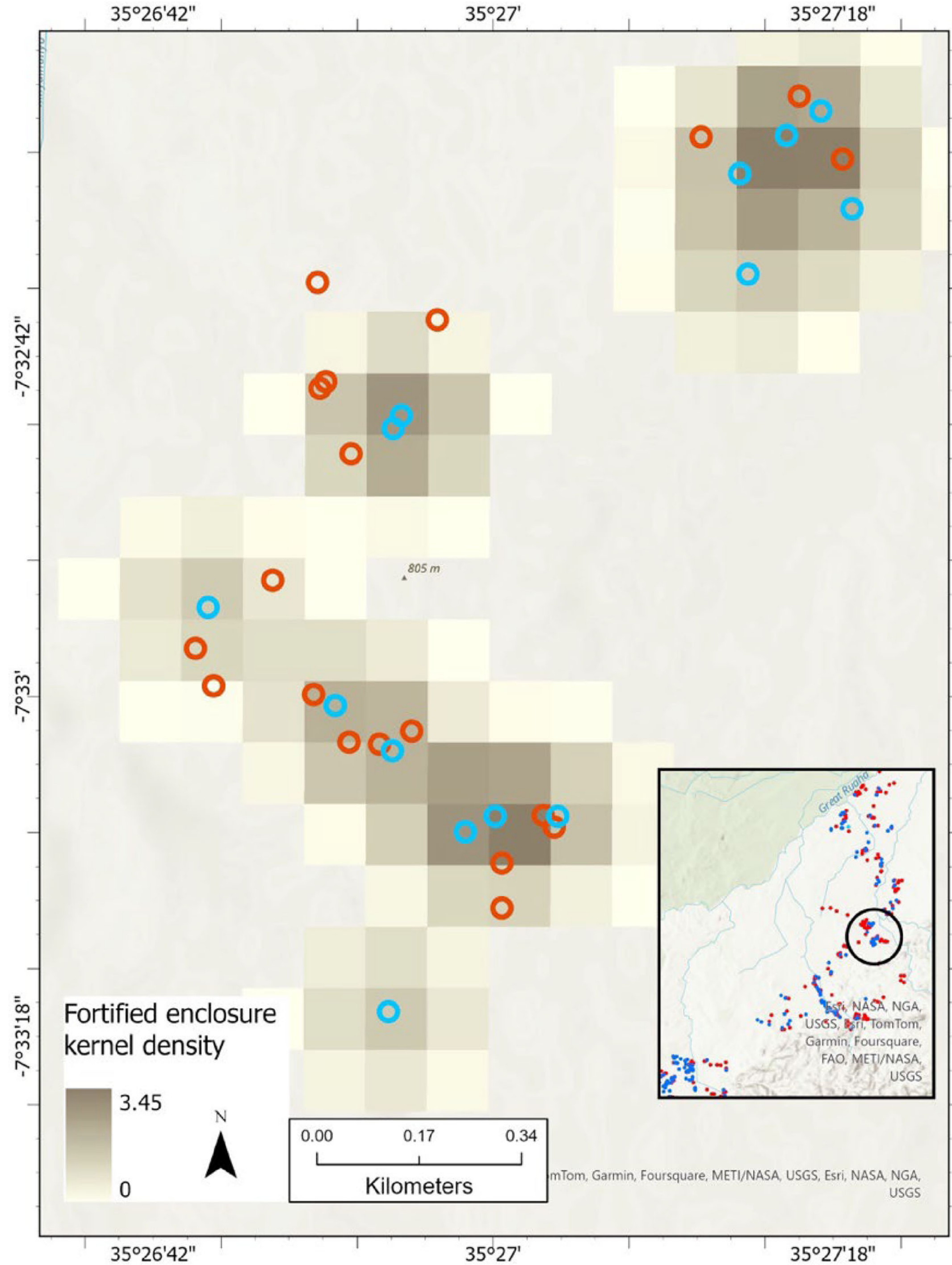

FIGURE 3 | Kernel density surface of estimated spillover effects of fortified enclosures. A subset neighborhood of households illustrates the spatial relationship of traditional-enclosure households (red circles) and the kernel density values estimating spillover effects from fortified enclosures (blue circles; tan-brown pixels), as of December 2022; 0 value pixels are transparent.

(Figure 4a; Table S2). Similarly, predation probability decreases for traditional-enclosure households as neighboring fortified-enclosure density increases, although this effect is weaker and less reliable (Figure 4b; Table S2). Predation probability decreases with linear distance from Ruaha National Park (Figure 4c; Table S2).

The landscape of enclosures does not remain fixed over time, as new fortified enclosures were constructed—from 115 to 251—during the study (Figure 2). A secondary model examines how newly constructed fortified enclosures affect predation probabilities in nearby traditional-enclosure households. Model estimates indicate no credible effect of time since new construction within a fortified-enclosure neighborhood (Figure 5; Table S3). This suggests that the presence of robust spatial spillover effects persists over time to reduce predation in the neighborhood of fortified enclosures.

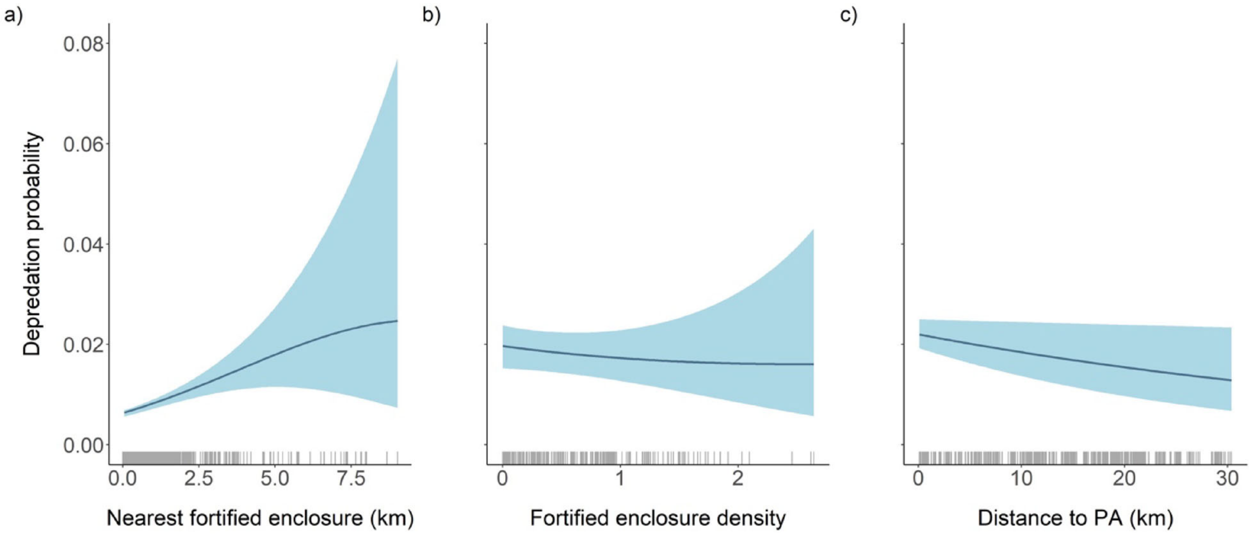

FIGURE 4 | Model estimates predicting the probability of carnivore predation on livestock in traditional-enclosure households from spillover effects of fortified enclosures. Posterior means and 95% credible intervals are plotted for the fixed effects of linear distance to the nearest fortified enclosure (a), fortified enclosure density (b), and distance to the protected area boundary (c) on the probability of predation in traditional-enclosure households. Observed predation events in traditional-enclosure households are displayed above the *x*-axis (gray ticks). Estimates are drawn from the joint-posterior density of the main Bayesian multilevel logistic regression model.

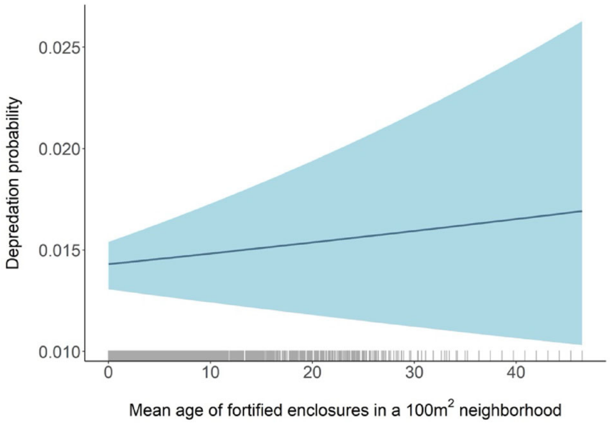

FIGURE 5 | Model estimate predicting the probability of carnivore predation on livestock in traditional-enclosure households from the time (months) since the construction of nearby new fortified enclosures. Posterior mean and 95% credible intervals are plotted for the fixed effect of mean age (months) of newly fortified enclosures on the probability of predation in traditional-enclosure households. Observed predation events in traditional-enclosure households are displayed above the *x*-axis (gray ticks). Estimates are drawn from the joint-posterior density of the secondary Bayesian multilevel logistic regression model.

4 | Discussion

Predation on livestock, and associated negative outcomes for humans and carnivores, significantly challenge global coexistence (Venumière-Lefebvre et al. 2022). To our knowledge, we present the first evidence suggesting that the beneficial spillover effects of a conservation intervention may reduce predation on livestock in the broader landscape beyond the target household or livestock operation. This evidence is drawn from data representing ca. 25,000 monthly household records and 846 reported predation events across 4 years in a region critical for the conservation of African carnivores.

As human land use expands, and in some cases, as carnivore populations recover, coexistence challenges increase (Van Eeden, et al. 2018; König et al. 2020). In RLL, community-managed conservation lands are important for wildlife habitat and buffer core protected areas, but predation on livestock negatively impacts people, which in turn can lead to intolerance and preventative and retaliatory carnivore killing (Dickman et al. 2014). We demonstrate higher predation closer to the national park boundary, but predation is still common across the landscape. This conflict feature in our system is akin to others in Tanzania (Salerno et al. 2016; Denninger Snyder et al. 2023) and globally, such as with tigers in India (Harihar et al. 2011) or gray wolves in western North America (Breck et al. 2023), where successful coexistence requires strategies to reduce predation on livestock. Our results support that not only are fortified livestock enclosures effective at reducing predation locally (Weise et al. 2018; Kissui et al. 2019; Grau et al. 2025), but that beneficial spillover effects may confer reduced predation for neighbors and that effects are likely durable over time. Furthermore, spillovers are most strongly felt by the nearest fortified-enclosure neighbors, more so than by the aggregate influence of multiple fortified enclosures, which has implications for maximizing their impact through strategic placement on the landscape.

The presence of spatiotemporal spillovers demonstrates the importance of examining complex systems dynamics to understand anticipated and unanticipated outcomes of conservation interventions. Indeed, our results raise the possibility that unrecognized spillover effects may account for some of the notable uncertainty regarding the effectiveness of various human–wildlife conflict mitigation strategies (Van Eeden, et al. 2018; Lorand et al. 2022), where social and landscape contexts strongly pattern outcomes for both people and wildlife (Killion et al. 2020).

The limited empirical work, thus far on spillovers, highlights how such effects may impact outcomes beyond the site of a local intervention. For instance, lethal control of wolves following predation on livestock may or may not deter future predations at the same site and could potentially displace predation to neighboring farms (Santiago-Avila et al. 2018). Similar detrimental spillovers to deflect predation to neighbors have also been reported with non-lethal strategies, such as with the use of fladry and guarding dogs in other wolf-livestock systems (Musiani et al. 2003) and with light deterrents around traditional livestock enclosures in East Africa (Lesilau et al. 2018), which calls into question their effectiveness at reducing conflicts in the wider landscape. Accounting for such effects will more clearly elevate trade-offs and interdependencies involved in conflict mitigation strategies.

The uncertain but potentially significant role that spillover effects play in coexistence points to important avenues for further research. For RLL and our study, the limited evidence base on spillover effects suggests no clear mechanism underlying the beneficial spillover we report. However, predator resource selection behaviors in a high-risk, high-effort landscape containing fortified enclosures may simply shift foraging to areas that maximize returns, that is, protected areas with higher natural prey availability (Wittmer et al. 2013). For carnivores engaged in area-restricted search, fortified enclosures may contribute to increased prey handling time, thereby lowering overall prey quality in an area, hastening search termination, and precluding negative spillovers locally (Lance et al. 2010; Dorfman et al. 2022). Similar adaptive foraging behaviors in response to food availability and risk have been observed in American black bears in urban landscapes when bear-proof trash cans are deployed as anti-conflict measures (Johnson et al. 2020). Indeed, perceived risk by carnivores will alter behavior in human-dominated landscapes (Oriol-Cotterill et al. 2015). We explored acute risk aversion, or fear, of initial construction of fortified enclosures that may deter carnivores as a possible explanation of beneficial spillovers (i.e., carnivores avoid the wider area following construction and perceived increased risk), yet the effect was weak and not credible, which suggests fear is unlikely to drive observed beneficial spillover effects. Nonetheless, we cannot rule out that sustained spillovers may still arise due to fear-driven responses by a subset of predator species in this multi-predator landscape (Lance et al. 2010; Elbroch and Treves 2023).

In addition, further research into spillover effects may uncover implications regarding tolerance and the scaling of interventions. Human tolerance for carnivores and damage-causing wildlife (i.e., people's attitudes and willingness to endure negative interactions) is key to supporting coexistence (Naughton-Treves 1998; Treves and Bruskotter 2014; Oriol-Cotterill et al. 2015). The beneficial spillover effects we report serve to amplify the reduction in predation achieved by fortified enclosures (Grau et al. 2025). Conflict reduction benefits livestock owners and increases their tolerance, which in turn is likely to reduce the potential for preventative or retaliatory carnivore killing (Kissui 2008; Dickman 2010; Kissui et al. 2019). Furthermore, we highlight the potential for social processes to support the spread of adoption of fortified enclosures and the transmission of tolerance following observed reductions in predation (Carter et al. 2020; Sibanda et al. 2021). Conversely, detrimental spillovers could influence the spread of intolerance and support for carnivore killing (Santiago-Avila et al. 2018). Together, these insights point to potential social–ecological feedbacks—where interactions among people and carnivores through spillover effects shape tolerance and intolerance—contributing to coexistence outcomes across landscapes.

Our study makes several assumptions. Observed declines in predation on livestock over time could also be due to declines in carnivore populations. While data describing carnivore populations are absent, we are unaware of adverse environmental or management conditions that could have affected such declines. Also, other antipredation strategies may have contributed additive effects to reduce predation, such as the use of livestock guarding dogs or light deterrents, although these are present in only a small number of households. In addition, data on carnivore species associated with predation events are absent but otherwise may have allowed for inference into the mechanism underlying observed beneficial spillovers. Finally, examination of spillovers is inherently spatially dependent; while beneficial spillovers likely reduced predation on livestock across our study system, we cannot rule out that predation was not displaced beyond this system.

Our results provide empirical evidence for policy and practice regarding tools to reduce human–carnivore conflicts. Grazing landscapes offer critical opportunities for maintaining biodiversity and supporting human livelihoods if conflicts can be effectively managed. This is true in East Africa and also in landscapes globally where humans, livestock, and carnivores overlap. Research shows that the effectiveness of antipredation strategies is too often short-term, context-dependent, and inferred from inappropriate study design (Van Eeden, et al. 2018; Killion et al. 2020; Khorozyan 2022). However, we demonstrate the importance of carefully examining interactions and feedbacks, which may help to elevate generalized outcomes. Our evaluation, where livestock enclosure fortification was carried out in tandem with extensive surveys to evaluate impacts, illustrates the value of robust designs and how systems approaches can inform cost-effective conservation planning. The additional integration of research on carnivore behavior and human tolerance will further improve the understanding of spillover effects and their role in the theory and practice of human–wildlife coexistence.

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Ethics Statement

Research conduct and ethics are approved by the Tanzania Commission of Science and Technology and Tanzania Wildlife Research Institute.

Consent

All research participants gave prior and informed consent.

Data Availability Statement

Data are available upon request from the corresponding author.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.