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Patterns of coyote predation on sheep in California: A socio-ecological approach to mapping risk of livestock-predator conflict

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Abstract

Conflict between livestock producers and wild predators is a central driver of large predator declines and simultaneously may imperil the lives and livelihoods of livestock producers. There is a growing recognition that livestockpredator conflict is a socio-ecological problem, but few case studies exist to guide conflict research and management from this point of view. Here we present a case study of coyote-sheep predation on a California ranch in which we combine methods from the rapidly growing field of predation risk modeling with participatory mapping of perceptions of predation risk. Our findings reveal an important selection bias that may occur when producer perceptions and decisions are excluded from ecological methods of studying conflict. We further demonstrate how producer inputs, participatory mapping, and ecological modeling of conflict can inform one another in understanding patterns, drivers, and management opportunities for livestock-predator conflict. Finally, we make recommendations for improving the interoperability of ecological and social data about predation risk. Collectively our methods offer a socioecological approach that fills important research gaps and offers guidance to future research.

KEYWORDS

carnivore conservation, grazing management, human dimensions of wildlife, human-wildlife coexistence, livestock-predator conflict, nonlethal control, participatory mapping, predation risk model, predator-prey, socio-ecological systems

1 | INTRODUCTION

Conflict between livestock producers and wild predators has been an intractable problem for millennia, with high stakes for both people and wildlife (Linnell, Odden, & Mertens, 2012). A globally-expanding human footprint ensures that predators and livestock continue to encounter one another on landscapes increasingly defined by scarcity, further intensifying conflicts (Drouilly, Nattrass, & O'Riain, 2018; Kuijper et al., 2016; Ogutu et al., 2016; Wolf & Ripple, 2017). For livestock producers, the presence of predators on a landscape often

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poses a material threat to lives and livelihoods, leading to preemptive or retaliatory killing of predators (Graham, Beckerman, & Thirgood, 2005; Muhly & Musiani, 2009; Treves & Karanth, 2003; Widman & Elofsson, 2018). These killings hasten the decline of large predators throughout the world and, combined with other drivers of loss, threaten their continued existence (Ripple et al., 2014). Large predator declines have far-reaching consequences, as their disappearance can trigger drastic ecosystem alterations and collapse (Estes et al., 2011) or engender social conflict (Brashares et al., 2014). While research has traditionally considered livestock-predator conflict from within disciplinary boundaries, there is a growing recognition that it is fundamentally a socioecological phenomenon, in which human beliefs and practices are reciprocally intertwined with ecological processes (Manfredo, 2008; Woodroffe, Thirgood, & Rabinowitz, 2005). Important theoretical groundwork has been laid, but there remains an important need for case studies that test socio-ecological methods for understanding livestock-predator conflict (Dickman, 2010).

The risks of livestock predation in space—both actual and perceived-are critical components of livestockpredator conflict with important potential to link its social and ecological dimensions. There exists a rich body of literature on the ecology of predation risk developed in natural systems (Gaynor, Brown, Middleton, Power, & Brashares, 2019; Hebblewhite, Merrill, & McDonald, 2005; Laundre, 2010; Sih, 1984). Ecologists have demonstrated that heterogeneous environments produce differential risks of predation, and that habitat characteristics, topography, ambush points, and other such landscape features are essential to the spatial patterning of predation risk (Brown, 1999; Gaynor et al., 2019; Trainor, Schmitz, Ivan, & Shenk, 2014). More recent research has applied these ecological theories to livestock predation (Kluever, Breck, Howery, Krausman, & Bergman, 2008; Kluever, Howery, Breck, & Bergman, 2009; Laporte, Muhly, Pitt, Alexander, & Musiani, 2010; Shrader, Brown, Kerley, & Kotler, 2008; Wilkinson et al., in press). In particular, the rapidly growing field of predation risk modeling uses statistical approaches from wildlife ecology to generate predictive, spatially explicit maps of livestock predation risk as it varies over a landscape (Miller, 2015; Treves & Naughton-Treves, 2004). Predation risk modeling is an especially suitable component of a socio-ecological case study as it is designed to be easily interpretable and actionable by producers and conservation practitioners, and its outputs are readily commensurable with quantitative social data (Miller, 2015; Miller, Jhala, & Schmitz, 2016; Suryawanshi, Bhatnagar, Redpath, & Mishra, 2013).

To understand the social dimensions of risk, it is critical to expand research on the risk perceptions of livestock

producers (Dickman, 2010; Kansky & Knight, 2014; Marchini & Macdonald, 2012; Suryawanshi et al., 2013; Treves & Bruskotter, 2014; Treves, Wallace, Naughton-Treves, & Morales, 2006). The conservation and recovery of large predators throughout the world will depend as much on perceptions and tolerance of them as the material risks they pose (Behr, Ozgul, & Cozzi, 2017; Treves & Karanth, 2003). Here we define "risk perceptions" as the set of beliefs held by a producer regarding the spatial variation in riskiness of the production landscape in terms of predation. Studies may rely entirely on perceptions to understand spatial patterns of livestock predation risk when other data is unavailable (Broekhuis, Cushman, & Elliot, 2017), and participatory maps of human-wildlife conflict have formed an increasingly important part of research and management toolkits for mitigating conflict (Kahler, Roloff, & Gore, 2012; Treves et al., 2006). These risk perceptions may (Miller et al., 2016) or may not (Suryawanshi et al., 2013) align well with empirical observations of predation likelihood, such as those produced by the predation risk models described above. Regardless of their accuracy, perceptions of risk are among the most important drivers of livestock husbandry decisions, including retaliatory actions against predators (Marchini & Macdonald, 2012; Moreira-Arce, Ugarte, Zorondo-Rodríguez, & Simonetti, 2018; Scasta, Stam, & Windh, 2017). Risk perceptions thus form critical components of producer decisions that actively shape the spatial pattern of predation risk by delimiting where livestock, and thus predation, may occur.

Predation risk is thus a function of both ecological characteristics and human decisions and the interactions between the two, meaning that an accurate understanding of livestock predation risk patterns must be gained through a socio-ecological lens. Ecological studies of livestock predation are still in need, and have important potential to reveal blind spots for livestock producers and managers regarding the circumstances and drivers of conflict (Wilkinson et al., in press). However, strictly ecological approaches may suffer from selection bias, in which available data do not represent the system, if they do not explicitly incorporate producer decisions regarding the distribution of livestock, and thus livestock predation. This is likely a widespread yet underappreciated methodological issue, as we have found no other studies describing it in the literature. Simultaneously, better approaches for quantifying risk perceptions and making them consistent with ecological models is a critical need for socioecological understandings of conflict (Dickman, 2010). We have also found no studies that have explicitly tested methods for improving interoperability between social and ecological data on predation risk. These notable research gaps stress the need for research that approaches

livestock-predator conflict from a comprehensive, socioecological point of view.

Here we present a case study on predation of domestic sheep (Ovis aries) by coyote (Canis latrans) in California that demonstrates the complementarity of social and ecological approaches to studying livestock-predator conflict and the cost of omitting either from consideration. First, we constructed fine-scale predation risk models using a unique 10-year dataset of livestock predation locations to examine environmental correlates of predation and produce a predictive map of predation risk. Second, we conducted a participatory mapping exercise with livestock producers to quantify and map producer risk perceptions. Third, we administered a questionnaire to the same producers to quantify perceived environmental drivers of predation risk. Finally, we compared the maps produced by each of these exercises to reveal the concordances and discrepancies between them, and, more importantly, to show the critical importance of socio-ecological approaches like this one to future conflict research.

2 | METHODS

2.1 | Study area

We focused our research on covote-sheep conflict in California, United States. As a pastured animal, sheep provide a particularly strong example of the role of husbandry decisions in determining predation risk. While cattle are too large to be prey for many local predator species, 28% of adult sheep losses and 36% of lamb losses in the United States in 2014-2015 were attributed to predators, and primarily to coyotes (USDA, 2015). California is the second-largest sheep producing state in the United States, and predation risk is a growing concern locally. After centuries of persecutions and extirpations (Reynolds & Tapper, 1996), a series of economic, legal, and cultural changes in California have led to large predator recoveries in the past few decades, heightening concerns about conflict (Berger, 2006; Bergstrom, 2017; Scasta et al., 2017). Coyotes have recovered more rapidly than other large predators, and their generalist diet and adaptability as predators have enabled the species to flourish in human-dominated spaces. These characteristics of predator, prey, and site make coyote-sheep conflict in California an ideal case study site for examining conflict in the 21st century.

We conducted our study at the University of California's 5,358 acre Hopland Research and Extension Center (HREC), located in the Mayacamas Mountains in Mendocino County, California. HREC lies between rural agricultural production and wildlands, bounded by remote Bureau of Land Management lands to the north and vineyards and suburban residences to the south. A mosaic of representative California Coast Range habitat types occurs on the property, including grasslands, oak woodlands, and chaparral (Figure 1).

Both coyotes and sheep occur at this site. Before the study site was donated to the University of California in 1951, HREC was a sheep ranch, and the university has maintained sheep on the site since its acquisition. During our study, 600 sheep on the site routinely grazed 34 of HREC's 60 total pastures. Pastures at HREC range in size from 3 to 263 ha, and are enclosed by fences of varying types, heights, and ages. Though other large predators including black bears (Ursus americanus), mountain lions (Puma concolor), and bobcats (Lynx rufus) occur on the site, coyotes account for the vast majority of all livestock predation, with estimates up to 98% (Blejwas, Sacks, Jaeger, & McCullough, 2002; Conner, Jaeger, Weller, & McCullough, 1998; Jaeger, 2004; Neale, Sacks, Jaeger, & McCullough, 1998; Scrivner, Howard, Murphy, & Hays, 1985). We reviewed logs recorded by livestock producers covering the past 50 years of husbandry and found no confirmed predations by any species except covote. Furthermore, neither staff nor agents of Wildlife Services contracted by HREC consider any other species as threats to the sheep at this site.

2.2 | Mapping observed and perceived predation risk

To form a socio-ecological understanding of predation risk at the study site, we employed multiple modes of analysis, using maps as a commensurable format for quantifying and comparing these spatially explicit approaches. First, we built predation risk models following the principles of resource selection functions to identify correlates of predation sites and make predictions about the spatial distribution of observed risk. Second, we developed participatory risk perception maps drawn by producers that represented their risk perceptions across the site's extent. Finally, we administered a questionnaire to examine how producers linked environmental and husbandry features to their risk perceptions, and we produced a map based on the answers provided in this exercise.

2.3 | Predation risk models of observed risk

2.3.1 | Data collection

We built predation risk models using livestock predation data collected by livestock producers since 2008. At HREC, WILEY Conservation Science and Practice

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FIGURE 1 The study took place at the Hopland Research and Extension Center (HREC), in northern California. This figure illustrates pasture boundaries, grazing areas, and major habitat types within the study site

when producers suspected a sheep predation has occurred, they filled out a data sheet detailing the location and time of the kill, the predator suspected, and whether enough evidence was available to confirm the species of predator. Producers marked carcass locations on a topographic map with 10 m contour intervals and demonstrated excellent knowledge of the geography of the site. When we validated 10 test sites by returning to them with a GPS, we found mapped carcasses to be within the GPS error (10 m) of their reported location.

In this analysis, we included only livestock predations for which producers felt there was sufficient evidence to confirm the predator species. Additionally, we excluded events in which producers did not provide a spatial location or in which confidence in that location was low (e.g., signs of a carcass being dragged after the kill). This filtering yielded n = 91 predation events.

We created a database of 40 variables describing the environment at and around the site of each predation event (Supporting Information Table S1). We included variables that we hypothesized to affect the spatial pattern of predation risk based on existing research on coyotesheep predation and discussions with producers at the study site. We included human presence and husbandry, topography, habitat, and pasture characteristics. We imported all data to ArcGIS as either 10 m rasters or pasture-level vectors (Supporting Information Table S2; ESRI, 2018). This resolution reflected the approximate error expected in the location of predation events by staff, and the use of data at this resolution allowed us to explore fine-scale variation in patterns of attack likelihood.

2.3.2 | Statistical modeling

Following methods from other predation risk modeling studies (Miller, 2015; Treves, Martin, Wydeven, & Wiedenhoeft, 2011) we built predation risk models based on the approach of resource selection functions (Boyce, Vernier, & Nielsen, 2002). Resource selection functions

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typically predict animal habitat use based on a logistic regression comparing "use" locations drawn from observations or telemetry to "nonuse" locations, where animals could have but did not occur. In our case, "use" locations were the 91 sites of sheep predation by coyotes, and "nonuse" locations were 600 randomly generated points (using the Create Random Points tool in ArcGIS) occurring within pastures where sheep were grazed.

We modeled attack likelihood from the use and nonuse points based on the 40 variables collected at each site using logistic regression in the program R (R Core Team, 2018). We used the "glmer" function in the lme4 package and included pastures as a random effect in our analysis to account for differences in pasture residence times. We used a hypothesis-driven approach to winnow down our large number of variables. We grouped variables thematically into categories of human presence and husbandry, topography, habitat, and pasture characteristics. We used model selection in a maximum likelihood framework to determine the most influential variables within each group (Burnham & Anderson, 2002). We maintained all variables that were included in models within 2 delta AIC of the top model. We then combined these variables into a single model, and again used a maximum likelihood model selection approach to rank models. When we excluded nonconverging models, a single top model remained, which was also the most parsimonious model. We calculated a variance inflation factor for all retained variables and confirmed that multicollinearity was not present in retained variables.

We tested the robustness of this model by bootstrapping a calculation of the area under the receiver operating characteristics curve (AUC) (Pearce & Ferrier, 2000). We split the data, with 80% as training and 20% as testing data, and calculated the AUC 100 times using the "performance" function in the ROCR package in R, generating a range of values, a mean, and a standard deviation for assessing goodness of model fit.

| TABLE 1 | Spatial variables for three models | of livestock predation risk |
|---------|------------------------------------|-----------------------------|
| | 1 | 1 |

| Variable | Predation risk model | Participatory map | Questionnaire score (1–5) |
|--------------------------------------|----------------------|-------------------|---------------------------|
| Habitat | | | |
| Chaparral area within 120 m | 0.40 | | 3.50 |
| Proportion of chaparral in a pasture | | | 4.00 |
| Vernal pool area within 120 m | 0.26 | | 1.13 |
| Woodland area within 120 m | | | 2.63 |
| Grassland area within 120 m | | -0.23 | 2.63 |
| Proportion of grassland in a pasture | | | 4.00 |
| NDVI | -0.48 | | 2.50 |
| Distance to water (squared) | -0.33 | | 2.00 |
| Distance to habitat patch edge | 0.27 | | 1.38 |
| Topography | | | |
| Ruggedness (500 m window) | -0.95 | | 3.63 |
| Ruggedness (30 m window) | 0.74 | 0.79 | 3.71 |
| Pasture characteristics | | | |
| Pasture size | | 2.47 | 3.67 |
| Perimeter to area ratio of pasture | | | 2.38 |
| Human presence and husbandry | | | |
| Height of nearest fence | -0.54 | | 3.38 |
| Condition of nearest fence | | | 3.75 |
| Distance to bedding sites | | | 3.38 |
| Distance to site boundary (squared) | -0.35 | | 1.13 |
| Average number of guardian dogs | | -0.58 | 4.75 |
| Distance to adjacent BLM property | | | 3.13 |

Note: Values for the predation risk model (logistic regression) and participatory map (linear regression) show estimates from the top models of these analyses. Values for the questionnaire score show the mean of respondent answers on a 1–5 scale regarding the importance of each variable to livestock predation from not important (1) to critically important (5). Blank boxes indicate that variables were not retained in model selection.

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Using the "predict" function in the car package in R, we mapped the results of this model across the extent of the study site. We reclassified the resulting 0–1 risk probabilities using two different schemes: an equal interval classification with low (0–0.33), medium (0.33–0.67) and high (0.67–1.0) values and a geometric interval with low (0–0.11), medium (0.11–0.33), and high (0.33–1.0) values. We initially chose an equal interval classification to match the format in which we asked livestock producers to share their perceptions of risk (described below). However, our initial results suggested that producers might have a low tolerance for risk, making a geometric interval that allows for more high-risk areas a better model analog.

Our discussions with producers led us to hypothesize that risk perceptions might be driven by the riskiest sites in a given pasture. Thus, we also created a coarser model at the pasture level in which risk across an entire pasture was defined by the riskiest 10 m cell within it.

2.4 | Participatory maps of risk perceptions

We invited all 10 available current and former livestock producers at the study site to map their risk perceptions across the study site, in both grazed and ungrazed pastures. We recognize that this sample size is perhaps not large enough to represent the full variation of perceived risk across producers in the region. However, it likely captures well the experience of producers making management decisions at the study site and suitably demonstrates our general approach. Of the producers invited to participate, nine agreed and one declined. We first conducted unstructured interviews with each producer. These interviews informed the breadth of variables included in our predation risk model (described above), established rapport with the producers, and primed them to think about how attack likelihood varies in space.

We presented each producer with a 150 cm \times 75 cm hardcopy map of the study site showing a high-resolution aerial imagery base map, pasture boundaries, roads, and other major identifying landmarks. We asked producers to draw areas of high, medium, and low risk for sheep with regard to coyote predation using red, yellow, and green permanent markers respectively (Supporting Information Figure S1). We clarified that these categories should be proportional to one another, such that they might be translated to a scale ranging from 1 to 3. We allowed interviewees to include as much detail in their maps (i.e., at any spatial resolution) as they felt necessary to represent risk gradations across the landscape. We digitized these hand-drawn perception maps in ArcGIS and assigned each color a score of 1 (low risk), 2 (medium



FIGURE 2 Spatial variation in likelihood of coyote predation on sheep, as predicted by the top predation risk model, classified into three categories using (a) an equal interval and (b) a geometric interval. While we asked producers to score risk according to an equal interval classification, the geometric interval appears to better replicate low risk tolerances and high sensitivities in increases in risk experienced by producers. Inset blowup maps, framed in blue, highlight areas of high predicted risk, according to the predation risk model

risk), or 3 (high risk). We combined these individual maps into a summary raster at 10 m resolution, with each cell representing the mean risk score across all interviewees.

We also identified environmental correlates for this summary risk perception map. Using ArcGIS, we generated 2,000 random points at the study site, each with a value (1, 2, or 3) drawn from the summary risk perception map. We conducted linear regression and model selection with the 40 environmental variables described above and in Supporting Information Table S1 to determine what environmental features were most strongly associated with perceptions of predation risk.

2.5 | Questionnaire

To go beyond producer intuition reflected in participatory maps and further explore the drivers of perceptions of predation risk, we sent a follow-up questionnaire to all producers we interviewed. We presented them with a list of environmental and husbandry features that had been mentioned in unstructured interviews or included in our predation risk model. We asked them to rank on a 1–5 scale from not important (1) to critically important (5) how influential each feature was in determining the predation risk of a site. We calculated means of these individual scores for each feature and used these means as weights of their corresponding raster layers. We summed these weighted rasters to produce a single 10 m raster layer that represented a questionnaire-based spatial model of perceived risk. As with our predation risk model, we reclassified the range of values produced in this exercise using both equal interval and geometric interval classification schemes to compare their fit with the participatory maps of risk perception.

2.6 | Comparing approaches

We classified data across these three approaches (predation risk modeling, participatory perception maps, and questionnaire) into the same categories of low (1), medium (2), and high (3) risk. This enabled us to directly compare differences across these three models by subtracting one model from another using the raster



FIGURE 3 Summarized risk perception map, depicting the spatial variation in likelihood of coyote predation on sheep, as perceived by livestock producers. We took mean scores of individual maps in which we asked producers at the study site to draw the risk of livestock predation in equal categories of low (1), medium (2), and high (3) risk at the study site 8 of 15

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calculator in ArcGIS. This exercise produced 10 m raster layers with values ranging from -2 to 2. A value of 0 indicates agreement between models; negative values indicate that perceptions show higher values of risk than the compared model; positive values indicate that perceptions show lower values of risk than the compared model.

3 | RESULTS

3.1 | Predation risk models

The top predation risk model retained ten variables (Table 1 and Supporting Information Table S2). Our bootstrapped AUC results ranged from 0.72 to 0.94, with a mean value of 0.86 and a standard deviation of 0.04, indicating a strong model fit (Pearce & Ferrier, 2000).

When we used this model to predict the spatial variation in predation likelihood across the study site, we found that most of the site was scored as low risk (Figure 2). When an equal interval classification was used, 96.0% of the site received a score of 1 (low risk), 3.8% of the site received a score of 2 (medium risk), and only 0.2% received a score of 3 (high risk). When a geometric interval was used, there was a larger percentage of high (4.0%) and medium (28.3%) scores on the site, but low risk areas (67.7%) still dominated. Both of these maps identify a few salient high-risk features, including steep-sided ravines highlighted in the blowup maps in Figure 2.

3.2 | Participatory perception maps

In contrast with the results of the predation risk models above, the summary risk perception map codes the large majority of our study site as high risk (Figure 3). This summary map scores 82.1% of the study site as high risk, 14.1% as medium risk, and 3.8% of the site as low risk. Only 7 of the study site's 34 grazed pastures are coded as predominantly high risk in this summary perception map. Only one pasture that is not currently grazed is coded as predominantly medium risk, and none of the ungrazed pastures are coded as predominantly low risk (Figure 3). Producers were largely in consensus with their designations of perceived risk, with only a few areas of disagreement occurring in some of the more frequently grazed pastures.

Linear regression modeling of the summarized participatory map produced a parsimonious model which retained only four variables (Table 1). Pasture size was by far the variable most strongly associated with high risk perceptions. Pastures with more guard dogs and a higher proportion of grassland were associated with lower risk perceptions, while ruggedness within 30 m was associated with higher risk assignments.



(a)

with risk. We used mean questionnaire scores regarding the importance of environmental variables in driving risk to weight spatial layers and produce summary maps. (a) 10 m resolution map using a geometric interval to reclassify results. (b) Pasture-level map using a geometric interval to reclassify results

(b)

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3.3 | Questionnaire

Mean questionnaire scores (Table 1) indicated that producers roundly regarded the number of guard dogs in a pasture as the most important factor in determining predation risk (mean score 4.8 out of 5). Producers also gave high scores to ruggedness within a 30 m window (3.7) and 500 m window (3.6), as well as to the proportion of chaparral (4.0) and grassland (4.0) in a pasture. The condition (3.8) and height (3.4) of the nearest fence also received high mean scores. While producers scored pasture size highly (3.7), it did not rank at the top of variables in this questionnaire as it did in the linear regression of the participatory map scores.

- (a) Perception minus predation risk model
- (b) Perception minus maximum predation risk model value per pasture



FIGURE 5 Differences in spatial patterns of risk between the summary perception map and other analyses presented in this study. Scores of 0 indicate no difference. Scores of +2indicate areas of high disagreement, where risk perceptions are high but comparing maps show low risk. Scores of -2 also indicate areas of high disagreement, but they depict areas where risk perceptions are low and comparing maps show high risk. (a) Risk perceptions minus our predation risk model reclassified using a geometric interval. (b) Risk perception minus our risk perception model, where the highest model value in each pasture was applied to the entire pasture. (c) Risk perception minus questionnaire scores mapped at 10 m resolution and reclassified using a geometric interval. (d) Risk perception minus questionnaire scores mapped at the pasture level and reclassified using a geometric interval

As with the predation risk model results above, we found stark differences in mapping the results of questionnaire scores at a 10 m resolution using an equal interval compared with a geometric interval. The former coded most of the study site as low or medium risk with only small pockets of high risk, while the latter displayed only a few areas of low risk among large areas of medium and high risk (Figure 4). The questionnaire scores we mapped at the pasture scale yielded larger areas of high and low risk, with medium risk covering a smaller area compared to the 10 m resolution map (Figure 4).

3.4 | Comparison of models and perceptions

There were stark differences between the predation risk models and the summary participatory risk map (Figure 5). Even when we applied a geometric interval, only 8.7% of our study site showed agreement (a difference of 0) between these two maps (Figure 5a). Across 57.0% of the study site, perceptions indicated high risk where the predation risk model indicated low risk (a difference of +2), and only 3.0% of the site featured predation risk model scores that were higher than perceptions (differences of -1 or -2; Figure 5a). When we applied the highest predation risk model score to its entire containing pasture, we found much higher areas of agreement with perception maps (Figure 5b). Using the predation risk model reclassified by geometric interval, we found that areas with a difference of 0 cover the majority of the study site (81.2%), while strong disagreement (differences of -2 or +2) was comparatively rare (3.2% and 0.9%, respectively).

Mapped questionnaire scores showed large areas of agreement with the summary perception map (Figure 5). When mapped at a 10 m resolution using a geometric interval to reclassify results, we found 62.0% of our study site had a difference of 0, and less than 1.0% showed strong differences of -2 or +2 (Figure 5c). Questionnaire scores mapped at the pasture level showed even larger areas of agreement with perception maps, with 75.0% of the study site having a difference of 0. Strong differences of -2 or +2 were also rare (<1.0%; Figure 5d). Agreement was most widespread in ungrazed pastures, while grazed pastures had greater areas of difference, including the only pasture with a majority of its area characterized as +2.

4 | DISCUSSION

This case study examines novel approaches by which to combine ecologically-driven predation risk models and

producer risk perceptions. The similarities and differences between the multiple maps we produced demonstrate the complexity of understanding livestock predation risk and the utility in applying socio-ecological approaches to managing human-wildlife conflict. Our results contribute several important findings, both in terms of specific management takeaways for the study site and broader guidance for future research and management of conflict from a socio-ecological perspective. The strong contrast between predation risk models and producer maps of risk perceptions highlights shortcomings of relying solely on either approach, demonstrates opportunities for applying these approaches in tandem, and reveals an important but often overlooked case of selection bias. The strong agreement between pasturelevel models and producer perceptions (Figure 5b,d) offers a window into the scale at which producers conceptualize risk and points to potential opportunities for targeted management interventions at fine scales. Our different methods highlight diverse drivers of risk, which suggests that ecologically-driven models and producer perceptions complement one another. Finally, our examination of different risk classification systems for our models offers further insight into the risk perceptions of producers and provides guidance for connecting social and ecological data on predation risk.

The most striking contrast among the different approaches to quantifying risk of livestock predation was between the predation risk model, which classified much of our study site as low risk, and the summary risk perception map, which revealed that producers consider most of the site as high risk (Figure 5a). While previous research has taken such discrepancies to indicate misunderstandings in the perceptions of producers (Gillingham & Lee, 2003; Suryawanshi et al., 2013), we propose a different interpretation of the results at this study site. Producer familiarity with the geography and ecology of the study site appears to be high, as evidenced by the accuracy of their mapping of carcass locations in data forms at the study site. Additionally, questionnaire answers reflect producers' understanding of the underlying drivers of their own risk perceptions, and these answers map well onto their intuitive drawings of risk perceptions (Figure 5c,d). This consistency suggests that producers are familiar enough with the site and its ecology to make accurate causal links between perceived drivers of risk and its patterning in space. We find it unlikely that producers with such site familiarity would misidentify the patterns of risk as severely as the contrast between the predation risk model and the risk perception maps might suggest.

Therefore, we instead suggest that this contrast highlights an important form of selection bias that is often overlooked in livestock predation research. Risk perceptions are an important driver of producer decisions (Marchini & Macdonald, 2012; Moreira-Arce et al., 2018; Scasta et al., 2017). Producers at our site avoided grazing livestock in pastures they perceived to be high risk, and grazed almost all the sites they perceived to be low or medium risk (Figure 3). Almost half of the study site was excluded from grazing due to predation concerns, including the largest pastures, which producers associated with high risk. These producer decisions about husbandry, which are powerfully driven by their risk perceptions, thus have a strong effect on where livestock predation can occur. The data that we used to build our predation risk model were thus already exposed to selection bias by these perception-driven producer decisions. This kind of selection bias has been identified in the ecology of predation risk (Moll et al., 2017) and explored more deeply in other fields (Hernán, Hernández-Díaz, & Robins, 2004), but it requires greater attention in the field of livestockpredator conflict. This selection bias likely affects many study systems, especially those, like this study site, where animals are pastured, producers have freedom to use or avoid areas they deem risky, and where models like ours extrapolate findings to areas that producers have chosen to avoid.

Due to this selection bias, we believe inherent patterns of risk at the study site are best identified through a combination of producer risk perceptions and the predation risk model. In areas that producers have already selected against, producer risk perceptions are likely the most accurate reflections of inherent landscape risk. However, within pastures that producers have chosen to graze, predation risk models can make an important contribution to understanding risk, especially at fine spatial scales. Many producers chose to draw their risk perception maps by identifying risk for entire pastures (Figure 3). When we applied each pasture's highest value from the predation risk model to the entire pasture, there was strong agreement between this model and risk perceptions (Figure 5b). This agreement suggests that producers may subscribe to a similar process in evaluating risk, taking a pasture's riskiest elements and applying them to the whole. Interestingly, this line of thinking creates opportunities for targeted, fine-scale management interventions. Within grazed pastures, the predation risk model does not suffer from the selection bias described above, and can thus offer a fine-scale, subpasture window into patterns of predation risk. Identifying hotspots of risk within pastures may identify new management opportunities that would not emerge from a pasture-level management viewpoint. For example, the predation risk model identified a network of steep ravines in a pasture as high risk (Figure 2, inset blowup), representing one of the few areas where the predation risk model assigned a higher risk score than that of the risk perception map (Figure 5a). A site like this represents a strong candidate for targeted management and further research, such as through temporary fencing to cordon this potentially high-risk area (Macon, Baldwin, Lile, Stackhouse, & Rivers, 2018).

In addition to mapping spatial patterns of risk, we also identified environmental correlates of risk and risk perceptions. Here too, contrasts between risk perceptions and our predation risk model reveal opportunities for complementary socio-ecological insights. In the predation risk model, habitat variables explained the bulk of variation in likelihood of coyote predation on sheep (Table 1 and Supporting Information Table S2). Model results suggest that coyotes may use the cover of locally rugged terrain, dense surrounding chaparral, and neighboring properties with less aggressive predator management to initiate attacks on sheep. Strong associations between predation risk and vernal pools and water sources suggest that these features may concentrate livestock prey, especially in spring when the pools are fullest and lambs are most vulnerable. While canids are typically considered coursing predators, several of the variables of our predation risk model suggest that covotes may locally adopt ambush predation strategies when landscape features are amenable to this hunting approach (Preisser, Orrock, & Schmitz, 2007; Sacks & Neale, 2002). Interestingly, previous research has shown important connections between drought and conflict (O'Loughlin et al., 2012; Saberwal, Gibbs, Chellam, & Johnsingh, 1994), and given that our study took place during one of the worst droughts in California history (Griffin & Anchukaitis, 2014), the unusually dry conditions could be mediating this behavioral adaptation by concentrating livestock prey.

In contrast to the spatial risk map, which highlighted habitat variables associated with risk, producers considered husbandry factors as central determinants of risk, as shown in both the questionnaire answers and linear regression of the summary perception map (Table 1). During interviews, producers typically discussed habitat in the light of husbandry practices, rather than as meaningful in isolation. For example, producers stated that ruggedness and habitat mattered to the extent that they limited or facilitated guardian dog movements and sightlines for both sheep and producers. In contrast to the predation risk model, producers described coyotes as a coursing predator, susceptible to chase by dogs and reliant on grassland habitats and large pastures to successfully carry out attacks. The predation risk model thus points to specific sites and strategies for testing new management strategies for coyotes as an ambush predator,

especially during severe drought conditions. For example, producers might place additional guardian dogs or nonlethal deterrents at vernal pools and along property boundaries where coyotes appear to concentrate attacks. Beyond these specific recommendations, the predation risk model highlights predator adaptability, which, as other studies have shown, necessitates dynamic, adaptive management to mitigate conflict (Stone et al., 2017; van Eeden et al., 2018; Wilson, Bradley, & Neudecker, 2017).

One of the strongest points of disagreement between livestock producer perceptions and the predation risk model was the importance of guardian dogs. Producers repeatedly emphasized the importance of guardian dogs during interviews, and both questionnaire answers and the linear regression of the summary perception map further reflected their importance to producer risk perceptions. These perceptions are well founded by research, which has demonstrated the effectiveness of guardian dogs in reducing livestock predation (Andelt, 1992; Coppinger & Coppinger, 1988; Gehring, Vercauteren, Provost, & Cellar, 2010; Green, Woodruff, & Tueller, 1984; van Bommel & Johnson, 2012). The predation risk model did not retain guardian dogs as a predictor of risk, however, and it had only a very weak effect in intermediate models before its exclusion. This omission may mask its importance, and shed light on the difficulty of understanding livestock-predator conflict without input from producers. While our model takes the landscape as a static snapshot of a 10-year period, producers dynamically respond to conditions over the course of the year. They commonly deploy more guardian dogs in pastures that they perceive to be riskiest. If the producers are correct about both the high inherent risk of these pastures and the effectiveness of the dogs, then these countervailing effects may be in part responsible for masking the dogs from the predation risk model. Examples of the complexity of mapping risk are common in ecological studies (Gaynor et al., 2019; Moll et al., 2017), but deserve greater attention in the field of livestock-predator conflict. Here, understanding producer perceptions and their associated husbandry decisions reveals not only factors that models may omit, but also reveals a more dynamic landscape that is difficult to capture in a static model. We suggest that future risk mapping exercises account for ongoing management practices and interpret model results in consultation with producers.

Increasing exchange between disciplines when undertaking socio-ecological questions is an important goal for supporting future research and management of livestock predation (Dickman, 2010). We adopted multiple methodological approaches that we expected to facilitate easy and meaningful exchange between social and ecological data. To this end, we asked producers to conceptualize risk in equal intervals of low, medium, and high, and we classified our predation risk model and questionnaire data accordingly. However, we found that questionnaire data matched perception maps much better when we used a geometric interval (Figure 5c), which sets much lower thresholds for high risk. Our predation risk model also displayed greater agreement with perception maps when we used a geometric interval (Figure 5a), and we believe this is well supported by the psychology of risk perceptions. Risk perception and tolerance are difficult to internally quantify and are extremely context dependent (Starr, 1969). Risk perceptions of wildlife in particular are easily inflated by feelings of vulnerability and lack of control, which typify livestock production (Carter, Riley, & Liu, 2012; Naughton-Treves & Treves, 2005; Skogen, Mauz, & Krange, 2008). We recommend that ecologicallydriven risk models explore and potentially adopt geometric interval or other similar classifications of risk data to account for low risk tolerances and heightened perceptions of livestock predation risk among producers.

In this study, we address several important gaps in the science of livestock-predator conflict and develop a series of complementary methods for considering conflict as a socio-ecological process. Our comparisons of socioecological data demonstrate an important but unreported form of selection bias and stress the importance of incorporating producer perceptions and decisions to avoid inaccurate inferences resulting from this bias. Combining producer perceptions and model data has untapped promise for improving understandings of livestock predation risk. Such a combination should consider using producer perceptions in locations that producers deem too risky to graze livestock, while making targeted management interventions at fine scales based on predation risk model outputs. Additionally, predation risk models can reveal underlying ecological dynamics-in this case the identification of covotes adapting an ambush predation strategythat may then inform specific management responses. However, other important drivers of risk—in this case the presence of guardian dogs-may be masked in empirical models by dynamic husbandry practices on a complex ecological landscape. We offer a guideline for quantifying risk perceptions that better reflects the psychology of risk perceptions and promotes interoperability between social and ecological data. Involving livestock producers in the science of predator-livestock conflict from start to finish has great promise to produce the most accurate and actionable understandings of conflict and to build trust that will support both wildlife and human livelihoods.

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CONFLICTS OF INTEREST

We have no conflicts of interest to declare.

AUTHOR CONTRIBUTIONS

A.M., J.R.B.M., K.M.G., and J.S.B. developed the project concepts and methods. A.M., J.R.B.M., and K.M.G. developed conceptual and analytical frameworks. A.M. collected data, conducted analyses, created figures, and drafted the manuscript. A.M., J.R.B.M., and K.M.G. conducted interviews. A.M., J.R.B.M., K.M.G., and J.S.B. revised the manuscript for publication.

ETHICS STATEMENT

All methods regarding human subjects were reviewed and approved or exempted by the UC Berkeley Institutional Review Board.

DATA AVAILABILITY STATEMENT

The data collected for this project cannot be publicly shared as it could potentially heighten the risk for study species at the research site or violate the anonymity of research subjects.

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REFERENCES

- Andelt, W. F. (1992). Effectiveness of livestock guarding dogs for reducing predation on domestic sheep. Wildlife Society Bulletin, 20, 55–52.
- Behr, D. M., Ozgul, A., & Cozzi, G. (2017). Combining human acceptance and habitat suitability in a unified socio-ecological suitability model: A case study of the wolf in Switzerland. *Journal of Applied Ecology*, 54, 1919–1929.
- Berger, K. M. (2006). Carnivore–livestock conflicts: Effects of subsidized predator control and economic correlates on the sheep industry. *Conservation Biology*, 20, 751–761.
- Bergstrom, B. J. (2017). Carnivore conservation: Shifting the paradigm from control to coexistence. *Journal of Mammalogy*, 98 (1), 1–6.

Conservation Science and Practice

- Blejwas, K. M., Sacks, B. N., Jaeger, M. M., & McCullough, D. R. (2002). The effectiveness of selective removal of breeding coyotes in reducing sheep predation. *The Journal of Wildlife Management*, 66, 451.
- Boyce, M. S., Vernier, P. R., & Nielsen, S. E. (2002). Evaluating resource selection functions. *Ecological Modelling*, 157, 281–300.
- Brashares, J. S., Abrahms, B., Fiorella, K. J., Golden, C. D., Hojnowski, C. E., Marsh, R. A., ... Withey, L. (2014). Wildlife decline and social conflict. *Science*, 345, 376–378.
- Broekhuis, F., Cushman, S. A., & Elliot, N. B. (2017). Identification of human-carnivore conflict hotspots to prioritize mitigation efforts. *Ecology and Evolution*, 7, 10630–10639.
- Brown, J. S. (1999). Vigilance, patch use and habitat selection: Foraging under predation risk. *Evolutionary Ecology Research*, 1, 49–71.
- Burnham, K. P., & Anderson, D. R. (2002). Model selection and multimodel inference: A practical information-theoretic approach (2nd ed.). New York, NY: Springer.
- Carter, N. H., Riley, S. J., & Liu, J. (2012). Utility of a psychological framework for carnivore conservation. *Oryx*, *46*, 525–535.
- Conner, M. M., Jaeger, M. M., Weller, T. J., & McCullough, D. R. (1998). Effect of coyote removal on sheep depredation in Northern California. *The Journal of Wildlife Management*, 62, 690.
- Coppinger, R., & Coppinger, L. (1988). A decade of use of livestock guarding dogs. Proceedings of the Vertebrate Pest Conference, 13, 209–214.
- Dickman, A. J. (2010). Complexities of conflict: The importance of considering social factors for effectively resolving humanwildlife conflict. *Animal Conservation*, 13, 458–466.
- Drouilly, M., Nattrass, N., & O'Riain, M. J. (2018). Dietary niche relationships among predators on farmland and a protected area. *The Journal of Wildlife Management*, *82*, 507–518.
- ESRI. (2018). *ArcGIS desktop: Release 10.6.1*. Redlands, CA: Environmental Systems Research Institute.
- Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., ... Wardle, D. A. (2011). Trophic downgrading of planet earth. *Science*, 333, 301–306.
- Gaynor, K. M., Brown, J. S., Middleton, A. D., Power, M. E., & Brashares, J. S. (2019). Landscapes of fear: Spatial patterns of risk perception and response. *Trends in Ecology & Evolution*, 34, 355–368.
- Gehring, T. M., Vercauteren, K. C., Provost, M. L., & Cellar, A. C. (2010). Utility of livestock-protection dogs for deterring wildlife from cattle farms. *Wildlife Research*, *37*, 715.
- Gillingham, S., & Lee, P. C. (2003). People and protected areas: A study of local perceptions of wildlife crop-damage conflict in an area bordering the Selous Game Reserve, Tanzania. *Oryx*, 37, 1017.
- Graham, K., Beckerman, A. P., & Thirgood, S. (2005). Human-predator-prey conflicts: Ecological correlates, prey losses and patterns of management. *Biological Conservation*, 122, 159–171.
- Green, J. S., Woodruff, R. A., & Tueller, T. T. (1984). Livestockguarding dogs for predator control: Costs, benefits, and practicality. *Wildlife Society Bulletin*, 12, 44–50.
- Griffin, D., & Anchukaitis, K. J. (2014). How unusual is the 2012–2014 California drought? *Geophysical Research Letters*, 41, 9017–9023.
- Hebblewhite, M., Merrill, E. H., & McDonald, T. L. (2005). Spatial decomposition of predation risk using resource selection functions: An example in a wolf-elk predator-prey system. *Oikos*, *111*, 101–111.

Hernán, M. A., Hernández-Díaz, S., & Robins, J. M. (2004). A structural approach to selection bias. *Epidemiology (Cambridge,* MA), 15, 615–625.

- Jaeger, M. M. (2004). Selective targeting of alpha coyotes to stop sheep depredation. *Sheep and Goat Research Journal*, *19*, 80–84.
- Kahler, J. S., Roloff, G. J., & Gore, M. L. (2012). Poaching risks in community-based natural resource management. *Conservation Biology*, 27, 177–186.
- Kansky, R., & Knight, A. T. (2014). Key factors driving attitudes towards large mammals in conflict with humans. *Biological Conservation*, 179, 93–105.
- Kluever, B. M., Breck, S. W., Howery, L. D., Krausman, P. R., & Bergman, D. L. (2008). Vigilance in cattle: The influence of predation, social interactions, and environmental factors. *Rangeland Ecology & Management*, 61, 321–328.
- Kluever, B. M., Howery, L. D., Breck, S. W., & Bergman, D. L. (2009). Predator and heterospecific stimuli alter behaviour in cattle. *Behavioural Processes*, *81*, 85–91.
- Kuijper, D. P. J., Sahlén, E., Elmhagen, B., Chamaillé-Jammes, S., Sand, H., Lone, K., & Cromsigt, J. P. G. M. (2016). Paws without claws? Ecological effects of large carnivores in anthropogenic landscapes. *Proceedings. Biological Sciences*, 283, 20161625.
- Laporte, I., Muhly, T. B., Pitt, J. A., Alexander, M., & Musiani, M. (2010). Effects of wolves on elk and cattle behaviors: Implications for livestock production and wolf conservation. *PLoS One*, 5, e11954.
- Laundre, J. W. (2010). Behavioral response races, predator–prey shell games, ecology of fear, and patch use of pumas and their ungulate prey. *Ecology*, *91*, 2995–3007.
- Linnell, J. D. C., Odden, J., & Mertens, A. (2012). Mitigation methods for conflicts associated with carnivore depredation on livestock. In L. Boitani & R. A. Powell (Eds.), *Carnivore ecology* and conservation (pp. 314–332). Oxford: Oxford University Press.
- Macon, D., Baldwin, R., Lile, D., Stackhouse, J., & Rivers, C. K. (2018). Livestock protection tools for California ranchers. ANR Publication, 8598, 1–16.
- Manfredo, M. J. (2008). *Who cares about wildlife?* New York, NY: Springer.
- Marchini, S., & Macdonald, D. W. (2012). Predicting ranchers' intention to kill jaguars: Case studies in Amazonia and Pantanal. *Biological Conservation*, 147, 213–221.
- Miller, J. R. B. (2015). Mapping attack hotspots to mitigate humancarnivore conflict: Approaches and applications of spatial predation risk modeling. *Biodiversity and Conservation*, 24, 2887–2911.
- Miller, J. R. B., Jhala, Y. V., & Schmitz, O. J. (2016). Human perceptions mirror realities of carnivore attack risk for livestock: Implications for mitigating human–carnivore conflict. *PLoS One*, 11, e0162685.
- Moll, R. J., Redilla, K. M., Mudumba, T., Muneza, A. B., Gray, S. M., Abade, L., ... Montgomery, R. A. (2017). The many faces of fear: A synthesis of the methodological variation in characterizing predation risk. *The Journal of Animal Ecology*, 86, 749–765.
- Moreira-Arce, D., Ugarte, C. S., Zorondo-Rodríguez, F., & Simonetti, J. A. (2018). Management tools to reduce carnivore– livestock conflicts: Current gap and future challenges. *Rangeland Ecology & Management*, 71, 389–394.

- Muhly, T. B., & Musiani, M. (2009). Livestock depredation by wolves and the ranching economy in the Northwestern U.S. *Ecological Economics*, 68, 2439–2450.
- Naughton-Treves, L., & Treves, A. (2005). Socio-ecological factors shaping local support for wildlife: Crop-raiding by elephants and other wildlife in Africa. *People and Wildlife*, 2000, 252.
- Neale, J. C. C., Sacks, B. N., Jaeger, M. M., & McCullough, D. R. (1998). A comparison of bobcat and coyote predation on lambs in North-Coastal California. *The Journal of Wildlife Management*, 62, 700.
- Ogutu, J. O., Piepho, H.-P., Said, M. Y., Ojwang, G. O., Njino, L. W., Kifugo, S. C., & Wargute, P. W. (2016). Extreme wildlife declines and concurrent increase in livestock numbers in Kenya: What are the causes? *PLoS One*, *11*, e0163249.
- O'Loughlin, J., Witmer, F. D. W., Linke, A. M., Laing, A., Gettelman, A., & Dudhia, J. (2012). Climate variability and conflict risk in East Africa, 1990–2009. *Proceedings of the National Academy of Sciences of the United States of America*, 109, 18344–18349.
- Pearce, J., & Ferrier, S. (2000). Evaluating the predictive performance of habitat models developed using logistic regression. *Ecological Modelling*, 133, 225–245.
- Preisser, E. L., Orrock, J. L., & Schmitz, O. J. (2007). Predator hunting mode and habitat domain alter nonconsumptive effects in predator-prey interactions. *Ecology*, *88*, 2744–2751.
- R Core Team. (2018). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing Retrieved from http://www.R-project.org/
- Reynolds, J. C., & Tapper, S. C. (1996). Control of mammalian predators in game management and conservation. *Mammal Review*, 26, 127–155.
- Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., ... Wirsing, A. J. (2014). Status and ecological effects of the world's largest carnivores. *Science*, 343, 1241484.
- Saberwal, V. K., Gibbs, J. P., Chellam, R., & Johnsingh, A. (1994). Lion-human conflict in the Gir Forest, India. *Conservation Biology*, 8, 501–507.
- Sacks, B. N., & Neale, J. C. C. (2002). Foraging strategy of a generalist predator toward a special prey: Coyote predation on sheep. *Ecological Applications*, 12, 299–306.
- Scasta, J. D., Stam, B., & Windh, J. L. (2017). Rancher-reported efficacy of lethal and non-lethal livestock predation mitigation strategies for a suite of carnivores. *Scientific Reports*, 7, 14105.
- Scrivner, J. H., Howard, W. E., Murphy, A. H., & Hays, J. R. (1985). Sheep losses to predators on a California range, 1973–1983. *Journal of Range Management*, 38, 418.
- Shrader, A. M., Brown, J. S., Kerley, G. I. H., & Kotler, B. P. (2008). Do free-ranging domestic goats show "landscapes of fear"? Patch use in response to habitat features and predator cues. *Journal of Arid Environments*, 72, 1811–1819.
- Sih, A. (1984). The behavioral response race between predator and prey. *The American Naturalist*, *123*, 143–150.
- Skogen, K., Mauz, I., & Krange, O. (2008). Cry wolf1: Narratives of wolf recovery in France and Norway. *Rural Sociology*, 73, 105–133.
- Starr, C. (1969). Social benefit versus technological risk. *Science*, *165*, 1232–1238.

- Stone, S. A., Breck, S. W., Timberlake, J., Haswell, P. M., Najera, F., Bean, B. S., & Thornhill, D. J. (2017). Adaptive use of nonlethal strategies for minimizing wolf-sheep conflict in Idaho. *Journal* of Mammalogy, 98, 33–44.
- Suryawanshi, K. R., Bhatnagar, Y. V., Redpath, S., & Mishra, C. (2013). People, predators and perceptions: Patterns of livestock depredation by snow leopards and wolves. *Journal of Applied Ecology*, 50, 550–560.
- Trainor, A. M., Schmitz, O. J., Ivan, J. S., & Shenk, T. M. (2014). Enhancing species distribution modeling by characterizing predator-prey interactions. *Ecological Applications*, 24, 204–216.
- Treves, A., & Bruskotter, J. (2014). Tolerance for predatory wildlife. *Science*, *344*, 476–477.
- Treves, A., & Karanth, K. U. (2003). Human-carnivore conflict and perspectives on carnivore management worldwide. *Conservation Biology*, 17, 1491–1499.
- Treves, A., Martin, K. A., Wydeven, A. P., & Wiedenhoeft, J. E. (2011). Forecasting environmental hazards and the application of risk maps to predator attacks on livestock. *Bioscience*, 61, 451–458.
- Treves, A., & Naughton-Treves, L. (2004). Predicting humancarnivore conflict: A spatial model derived from 25 years of data on wolf predation on livestock. *Conservation Biology*, 18, 114–125.
- Treves, A., Wallace, R. B., Naughton-Treves, L., & Morales, A. (2006). Co-managing human-wildlife conflicts: A review. *Human Dimensions of Wildlife*, 11, 383–396.
- USDA. (2015). Sheep and lamb predator and nonpredator death loss in the United States, 2015 (pp. 1–52). Fort Collins, CO: USDA– APHIS–VS–CEAH–NAHMS.
- van Bommel, L., & Johnson, C. N. (2012). Good dog! Using livestock guardian dogs to protect livestock from predators in Australia's extensive grazing systems. Wildlife Research, 39, 220.
- van Eeden, L. M., Eklund, A., Miller, J. R. B., López-Bao, J. V., Chapron, G., Cejtin, M. R., ... Treves, A. (2018). Carnivore

Conservation Science and Practice

conservation needs evidence-based livestock protection. *PLoS Biology*, *16*, e2005577.

- Widman, M., & Elofsson, K. (2018). Costs of livestock depredation by large carnivores in Sweden 2001 to 2013. *Ecological Economics*, 143, 188–198.
- Wilkinson, C., McInturff, A., Miller, J. R. B., Gaynor, K., Calhoun, K., Karandikar, H., ... Yovovich, V. (in press). An ecological framework for contextualizing carnivore livestock conflict. *Conservation Biology*.
- Wilson, S. M., Bradley, E. H., & Neudecker, G. A. (2017). Learning to live with wolves: Community-based conservation in the Blackfoot Valley of Montana. *Human–Wildlife Interactions*, 11, 245–257.
- Wolf, C., & Ripple, W. J. (2017). Range contractions of the world's large carnivores. *Royal Society Open Science*, 4, 170052.
- Woodroffe, R., Thirgood, S., & Rabinowitz, A. (Eds.). (2005). People and wildlife: Conflict or coexistence? Cambridge: Cambridge University Press.

SUPPORTING INFORMATION

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

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