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From encounter to death: Which stages of predation are considered within livestock depredation research?

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ABSTRACT

The predation of livestock by carnivores, known as livestock depredation, negatively impacts livestock owners and predator conservation. Although various management interventions have been implemented globally, considerations of predator behaviour and predator-prey ecology have not generally been at the forefront of this development. Yet, an ability to predict how different predator species and livestock behave during a depredation event may lead to more evidence-based and tailored interventions with increased long-term effectiveness. We divided the depredation process into successive stages during which key predatory decision-making takes place, informed by the formative predator-prey theory developed by Lima and Dill (1990). These stages include *encounter*, *interaction*, *attack*, *capture*, and *death*. We then systematically reviewed the depredation literature to quantify research effort alignment with each stage. We found that the *death* stage was by far the most commonly assessed (96 % of reviewed studies, $n = 522$ of 548), with other stages considered four to 30 times less frequently. Only 1.5 % of reviewed studies ($n = 8$ of 548) made real-time visual observations or recordings of any of these stages. We describe the importance of considering the predatory process across each of these stages and discuss how current focus on the collection and analysis of post-hoc data following livestock death or proxy data may limit intervention effectiveness. We provide practical advice for the study of all stages, highlighting relevant methodologies and novel avenues of future research. Integrating ecological and behavioural principles into depredation research should lead to a better understanding of predator-livestock dynamics, and more effective interventions.

1. Introduction

The coupled growth of human populations and livestock production has increased the rates at which humans interact with wildlife (Michalski et al., 2006; Otuoma et al., 2009; Robinson et al., 2014). Attacks on livestock by predators, known as livestock depredation, can lead to human-predator conflict, which can affect livestock owners financially, psychologically, socially, and culturally (Ngowi et al., 2008; Zahl-Thanem et al., 2020; Braczkowski et al., 2023). In turn, these processes can be detrimental to conservation due to the injurious or lethal action taken against predators in prevention of, or in retaliation for, livestock depredation (Creel and Rotella, 2010; Mateo-Tomás et al., 2012; Ripple et al., 2014). Lethal responses to livestock depredation, however, are now increasingly accompanied by a range of non-lethal management interventions. Different interventions, such as light-producing devices around communities (Götz and Janik, 2016; Hall and Fleming, 2021), the enclosure of livestock (Samelius et al., 2021), or even protective collars around livestock's necks (Shivik, 2006), for example, aim to disrupt a depredation event at various stages of its advancement. The examples above would seek to dissuade the predator from approaching, attacking, and capturing livestock, respectively. However, it remains unclear how these stages, from an initial encounter between predator and livestock to the eventual death of the livestock, are behaviourally navigated by different predator species and whether current research efforts address this.

Various frameworks have broken down the pursuit of an individual prey by a predator into successive steps (Endler, 1991). One was developed by Lima and Dill (1990), roughly outlining five broad stages in the predation process including: *i*) *encounter*, *ii*) *interaction*, *iii*) *attack*, *iv*) *capture*, and *v*) *death*. At each stage, different events could either advance the process to the next stage or end the predation event altogether (Fig. 1). This and other similar frameworks have been used for a

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variety of purposes in wildlife ecology, such as modelling predation risk and studying anti-predator behaviours of prey at each of these stages (Lima and Dill, 1990; Caro, 2005; Hebblewhite et al., 2005). However, no such framework has, as yet, been adapted to livestock depredation research, despite its potential to shed light on the mechanistic underpinnings of livestock depredation events (Hoffmann et al., 2022). In particular, use of such a stage-based framework could aid in identifying depredation-specific behavioural patterns displayed by various predator species. It is reasonable to assume that understanding of predator pursuits of wild prey will often not directly apply to livestock depredation. The environments in which wild predation and livestock depredation occur vary considerably in terms of landscape structure, human densities, risk to predators, and physical obstacles to overcome (Valeix et al., 2012; Smith et al., 2017). Moreover, livestock are domestic animals which often have different anti-predator behaviours to wild prey species (Mignon-Grasteau et al., 2005; Beck et al., 2021).

Despite the evident differences between livestock and wild prey, livestock depredation is by definition a predation event. Thus, in much the same way that a wild predation event has been subdivided temporally, depredation can also be broken down into a series of stages during which key predatory and anti-predatory decisions are made, by predator and prey respectively. We therefore define the stages outlined by Lima and Dill (1990) within the context of livestock depredation (Fig. 2).

First, the *encounter* stage occurs when either predator or livestock first detects the other. Importantly, for detection to occur, either the predator or the livestock must be within the detection range of the other (i.e., an opportunity for encounter, Fig. 1). Due to reduced anti-predator instincts of livestock (Geffroy et al., 2020; Beck et al., 2021), in most situations the predator can be expected to detect the livestock first. Second, the *interaction* stage occurs when both predator and livestock have detected each other. As the predator is expected to often encounter the livestock first, as articulated in the description of the previous stage, the *interaction* stage will often constitute the detection of the predator by the livestock. This is represented by the event 'prey detects predator' in our adapted flowchart of the Lima and Dill (1990) model (Fig. 1). Oddly, this event was not featured in their original framework. Despite this, we believe that it is an important step in the process of livestock depredation, and have thus adapted the original framework to include the possibility of livestock detecting the predator at the *interaction* stage. This stage presents an opportunity for livestock to escape before being physically attacked or to dissuade the predator from attacking, though importantly the potential for escape is reduced in the case of enclosed livestock. Even in the case of a depredation event that does not lead to death, however, the *interaction* stage may have important non-lethal consequences on livestock. Non-lethal consequences might include curtailed feeding, decreased reproductive output, or lower quality of derived products, among other effects. Sometimes, this stage can be skipped entirely if livestock are unaware of the predator's presence until they are attacked (Fig. 1). Third, the *attack* stage occurs when the predator begins to actively pursue the livestock. If livestock are enclosed, this is the stage at which the predator breaches the barrier separating them. Fourth, the *capture* stage is the moment at which the predator physically contacts the livestock. In some instances, capture does not lead to death but to injury only. Finally, the *death* stage occurs when the livestock dies. It is either consumed by the predator or dies from its injuries without consumption, for example in the case of surplus killing or if the predator is chased away before consuming its prey.

At each of these stages, predator species are expected to show specific behavioural patterns and strategies to successfully reach the last stage of the process, the death of the livestock prey. We also expect that livestock of different types may display varying behaviours or reactions to predatory events. The study of predator and prey behaviour throughout the process of livestock depredation could effectively limit livestock deaths by permitting the design of interventions that are adapted to both the livestock present and the most conflict-causing predator species in the area. Although a framework of this type has not yet been adopted explicitly in depredation research, it may be that current research does nevertheless associate implicitly with these stages. Existing literature could then be used to extract, for instance, behavioural patterns displayed by different predator species throughout the depredation process. This could be subsequently used to identify the most useful species-specific interventions. However, in the event that

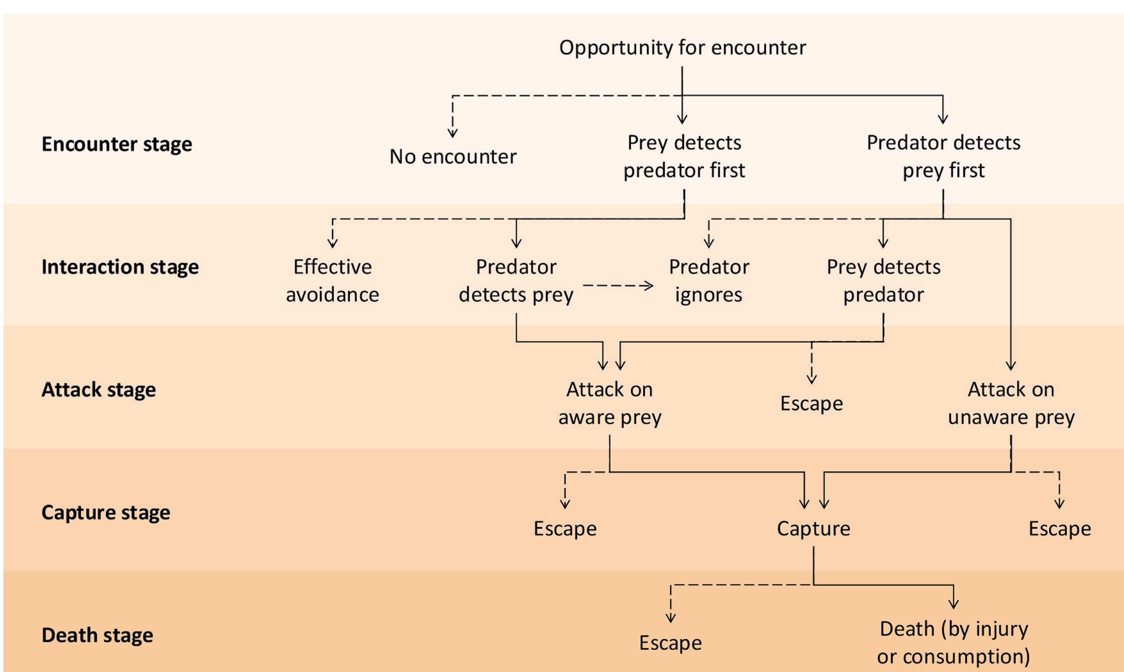

Fig. 1. Potential outcomes of an encounter between a predator and a prey individual, separated into five successive stages. Adapted from Lima and Dill (1990). The solid arrows lead to events that allow the depredation process to proceed, while the dashed arrows lead to events that end the depredation process before the death of the prey.

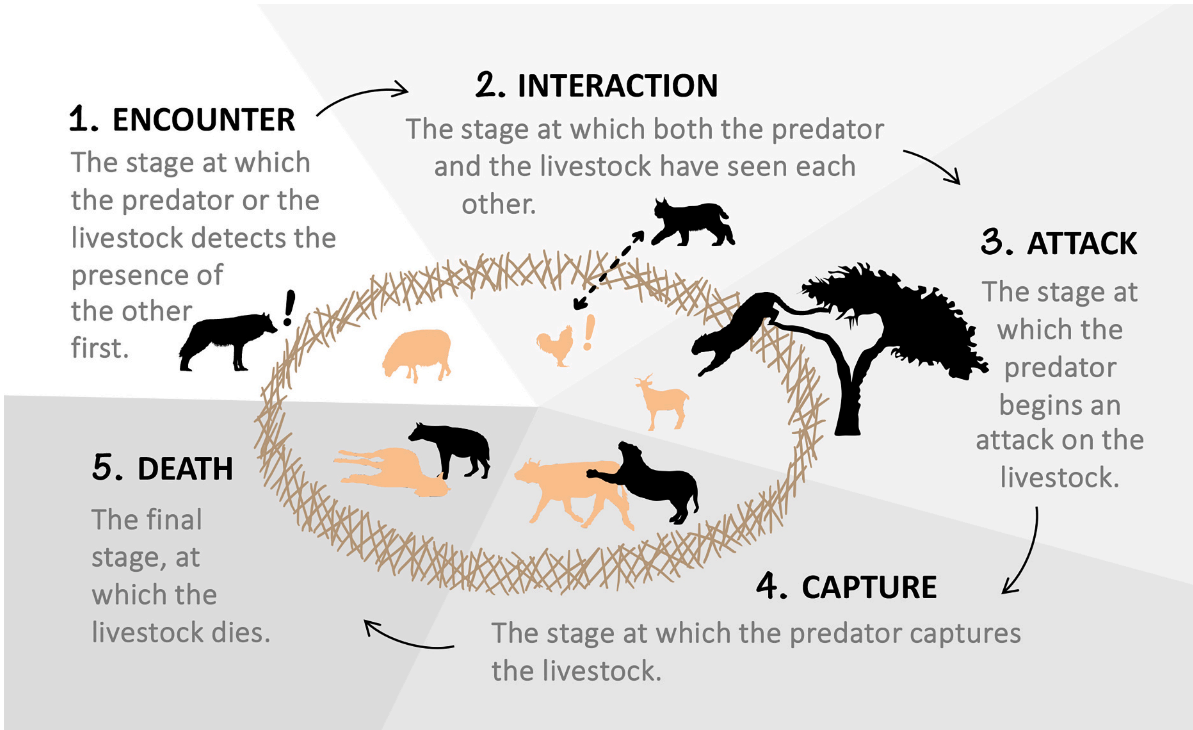

Fig. 2. Definitions and illustrations of the five stages of the livestock depredation process, adapted from the stages of the wild predation process, originally developed by Lima and Dill (1990).

existing research has not assessed depredation as a dynamic, multi-step predator-prey interaction, but rather shows a dependence on post-hoc data once livestock is already dead, the absence of information on pre-death predatory events may limit the development of tailored and evidence-based interventions. Here, we conducted a systematic literature review to determine the methods used and extent to which depredation research considers all stages of the livestock depredation process, as defined above.

2. Methods

On the 5th of May 2025, we conducted a literature search on the Web of Science Core Collection database. To execute this review, we carried out a topic search (i.e., titles, abstracts, and keywords of publications), with no date restrictions, using the following search string: (depredation OR "livestock predation") AND carnivor*. We first removed all duplicates from the literature returned. We then screened the remaining studies at the abstract and full-text stages following the inclusion-exclusion criteria that we present below.

2.1. *Eligibility of studies*

We first chose to retain studies that either reported novel data, or presented a novel analysis or simulation of data regarding livestock depredation events. Within this criterion, we only retained studies on the depredation of vertebrate livestock, which we define here as domesticated or semi-domesticated vertebrate animals kept in an agricultural context for consumption, derived products, or labour. We therefore excluded studies which solely focused on the predation of other domestic or human-kept animals, such as dogs or bees. Furthermore, we include within the umbrella of a "livestock depredation event" any event during which a predator kills, attacks, or encounters living livestock or objects meant to imitate living livestock with the purpose of eliciting natural predatory behaviours from the predator (e.g., livestock dummies or decoys). We therefore excluded studies which solely focused on the scavenging of livestock remains, as this was not considered to be a depredation event. Second, we only retained peer-reviewed studies, thus excluding book chapters as well as conference proceedings when it was not clear whether a peer review process had taken place. We retained studies from any journal with a peer-review process, including those that could be considered predatory, as there is no objective classification of predatory versus non-predatory journals. Third, we excluded studies which were narrative reviews, presented a conceptual framework, or were framed as a perspective article, opinion piece, or essay. In addition, we excluded systematic reviews of the literature, as well as meta-analyses. However, if any of these study types also presented novel data or a novel analysis of data, then they were retained. Fourth, we excluded studies if we encountered difficulties accessing their full text. Due to author limitations, we also excluded studies where no English-language version of the full text could be found.

Finally, we considered whether each remaining study used or reported, in its methods or results sections, data specifically relating to one or more of the stages of depredation described above. Such data could describe either realised encounter, interaction, attack, capture, or death events, or potential events through the use of proxy data. In this context, we define proxy data as indirect sources of data used by studies to infer information about a depredation stage, without collecting data on the occurrence of the stage itself. For example, studies might equate the overlap between a predator's home range and livestock herds to the occurrence of encounters between the two, without observing or verifying such occurrences. We provide further detail and examples of this below (see Sections 2.2.1 to 2.2.5).

Our initial search yielded 966 studies. Following the screening process we describe above, we retained 548 studies, published from 1997 to 2025, from which we then collected data. See Fig.S1 for a detailed breakdown of the number of studies remaining following each step of the screening process. A dataset of all excluded studies can be found in the Supplementary Material.

2.2. Data collection

For each of the 548 retained studies, we first recorded the system in which livestock depredation occurred including the location(s), country (ies), and the species (or higher taxonomic level where species was not specified) of the predator(s) involved. In instances in which several countries or predator species were assessed in a single study, we recorded all of them.

We then noted which of the five stages of livestock depredation were assessed in each study. As we provide the first framing of these stages for livestock depredation in this paper, we could not expect the specific stage names to be used in these studies. Instead, we critically examined the methods and results sections of each study and identified the corresponding stages using the definitions described above (see Fig. 2). Below, we present more detailed descriptions of the criteria with which we determined the stage(s) considered by each study. For every stage assessed, we recorded the manner in which it was studied, paying close attention to whether the stage was studied in real time (i.e., at the time of the event) using methods like visual recordings and observations or remote satellite/GPS tracking, or whether it was studied indirectly using post-hoc or proxy data. All data collected from each reviewed study can be found in the Supplementary Material.

2.2.1. Encounter

Studies making real-time observations of instances in which predators encountered livestock (e.g., in person, using camera traps, etc.), or tracking predators as they approach livestock were counted as studying the *encounter* stage. However, there are other, more indirect ways in which the *encounter* stage can be considered, for example using proxy data. Therefore, in this category we also included studies which used data to infer information about potential encounter events. For example, occupancy, distribution, or abundance data on predators, livestock, or both, can be used to infer locations or hotspots of potential encounters. This type of data can be compared to locations of realised depredation events to determine areas in which potential encounters are at a high risk of leading to livestock deaths. Another way in which abundance data can be used to study the *encounter* stage is by determining whether livestock are a preferred prey of a given predator species, by comparing their prevalence in the diet of the species to their local availability in the landscape (e.g., Jacobs' index). Additionally, studies framed as a test (using before/after or control/treatment data) of an intervention specifically aimed at reducing the frequency of predator-livestock encounters were also classed as studying the *encounter* stage, even if the test of the intervention was conducted using post-hoc data on livestock deaths. Studies reporting the presence of carnivores in or near communities or farms were only included if this data was specifically related to potential or realised encounters with livestock. Studies simply including livestock density as a variable to explain livestock depredation were not included as we did not consider that this provided enough data to estimate potential encounters with predators.

2.2.2. Interaction

Following our descriptions of the stages of livestock depredation, we classed studies as considering the *interaction* stage when they focused on livestock detections of predator presence. For example, this could include any study of non-lethal effects of interactions with predators on livestock.

2.2.3. Attack

An attack constitutes any active pursuit of livestock by a predator. This includes the breaching of barriers that separate predator from livestock. Any study related to the pursuit of livestock by predators was included as studying the *attack* stage. This could include, for example, studies testing the effectiveness of an intervention (using before/after or control/treatment data) specifically aimed at interrupting the predation sequence at the *attack* stage (e.g., bomas, fences, etc.). Studies testing the effectiveness of interventions that could act at any stage of the depredation process (e.g., livestock guarding dogs; LGDs, or herding) were attributed a stage based only on the type of data used to assess their effectiveness.

2.2.4. Capture

Studies were classed as considering the *capture* stage when they presented data either relating to livestock injuries, or to physical markers of capture. For example, we included in this category studies which reported levels of predator-caused livestock injury, or studies looking at strategies of capture by various predators (e.g., bite locations).

2.2.5. Death

Studies collecting, reporting, or making use of data relating to livestock deaths were classed as studying the *death* stage. This includes reports of numbers of dead livestock in specific areas (e.g., via interviews, official records, etc.), whether the aim of the study was to report levels of realised livestock depredation, or whether this data was then used for an analysis or a test of an intervention. A number of studies returned by our search reported results of questionnaire surveys or interviews of local communities which were affected by livestock depredation. In these cases, the studies were only included when quantitative data on one of the stages was reported or quantitative analyses were conducted in the Results section. For example, a study which exclusively reported questionnaire responses could only be listed as studying the *death* or *capture* stages if the results provided a measure of the intensity of the depredation events experienced by the respondents (e.g., number of events, number of livestock lost or injured, or percentage of respondents reporting these events), and reported on the predator species responsible for these depredation events. Additionally, an indication of the type of livestock affected or a breakdown of the circumstances of these events (e.g., how many took place at night, during the day, etc.) had to be included. Surveys that only reported anecdotal accounts of livestock depredation were excluded, as well as studies in which respondents only mentioned being affected by livestock depredation.

3. Results

Among the 548 reviewed studies of livestock depredation, the predator species most represented was the leopard (*Panthera pardus*; 29 %, $n = 160$ of 548; Fig. 3), followed by the wolf (*Canis lupus*; 29 %, $n = 158$ of 548; Fig. 3), and the lion (*Panthera leo*; 15 %, $n = 84$ of 548; Fig. 3). In total, 115 predator taxa were represented, including 96 different identified species (Table S1). The country most represented was India (12 %, $n = 64$ of 548), followed by the United States (8 %, $n = 42$ of 548), and Pakistan (7 %, $n = 41$ of 548). In total, 77 countries were represented (Fig. 4). Asia was the most represented continent in this literature (38 %, $n = 209$ of 548, 17 different countries; Fig. 4), followed by Africa (28 %, $n = 151$ of 548, 16 different countries; Fig. 4), Europe (16 %, $n = 87$ of 548, 32 different countries; Fig. 4), North America (11 %, $n = 62$ of 548, six different countries; Fig. 4), and South America (7 %, $n = 41$ of 548, six different countries; Fig. 4). Oceania was not represented in any of the reviewed studies (Fig. 4). Full lists of taxa and countries featured among this literature can be found in the Supplementary Material (Tables S1 & S2).

3.1. Representation of the stages of the depredation process

Around 66 % ($n = 364$ of 548) of the studies examined just one stage of the depredation process, while none studied all five stages (Fig. 5A). The most studied was the *death* stage, occurring in 96 % ($n = 522$ of 548) of studies (Fig. 5B; Table 1). The next most studied was the *encounter* stage, which featured in 26 % of studies ($n = 139$ of 548; Fig. 5B; Table 1). The *capture*, *attack*, and *interaction* stages were examined in 11 % ($n = 60$ of 548), 5 % ($n = 28$ of 548), and 3 % ($n = 16$ of 548) of the

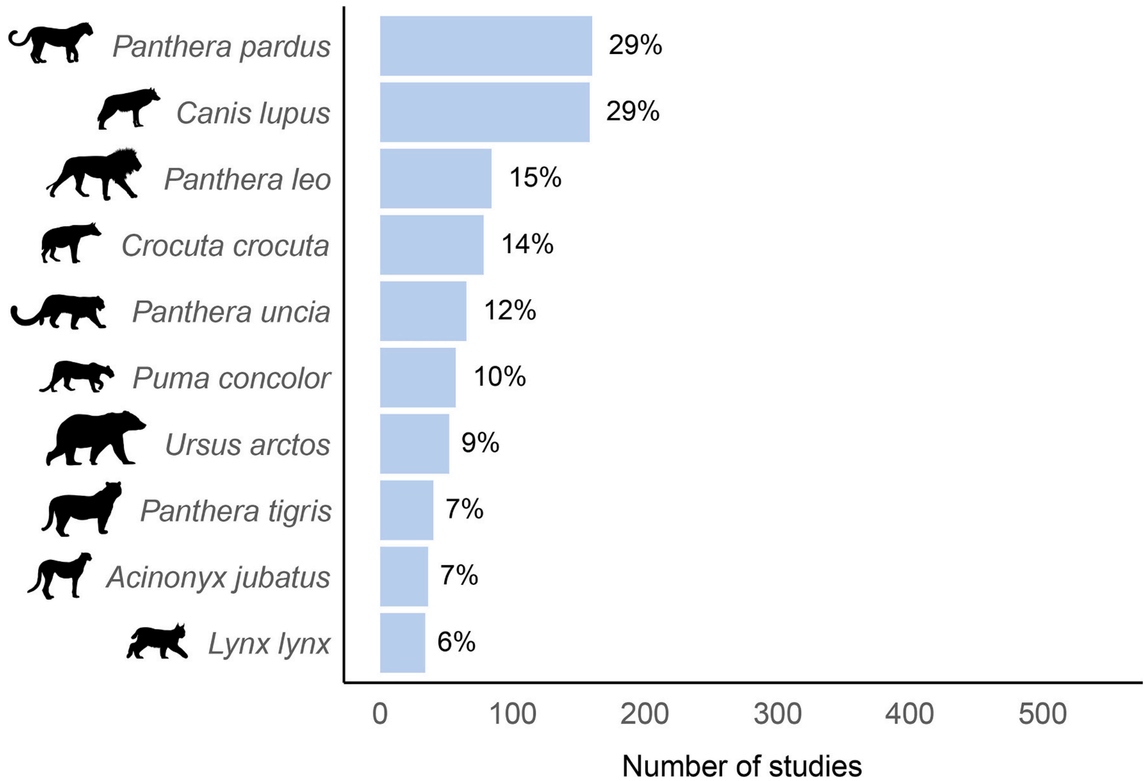

Fig. 3. The ten most represented predator species among 548 reviewed studies of livestock depredation (1997–2025), ranked from most to least studied.

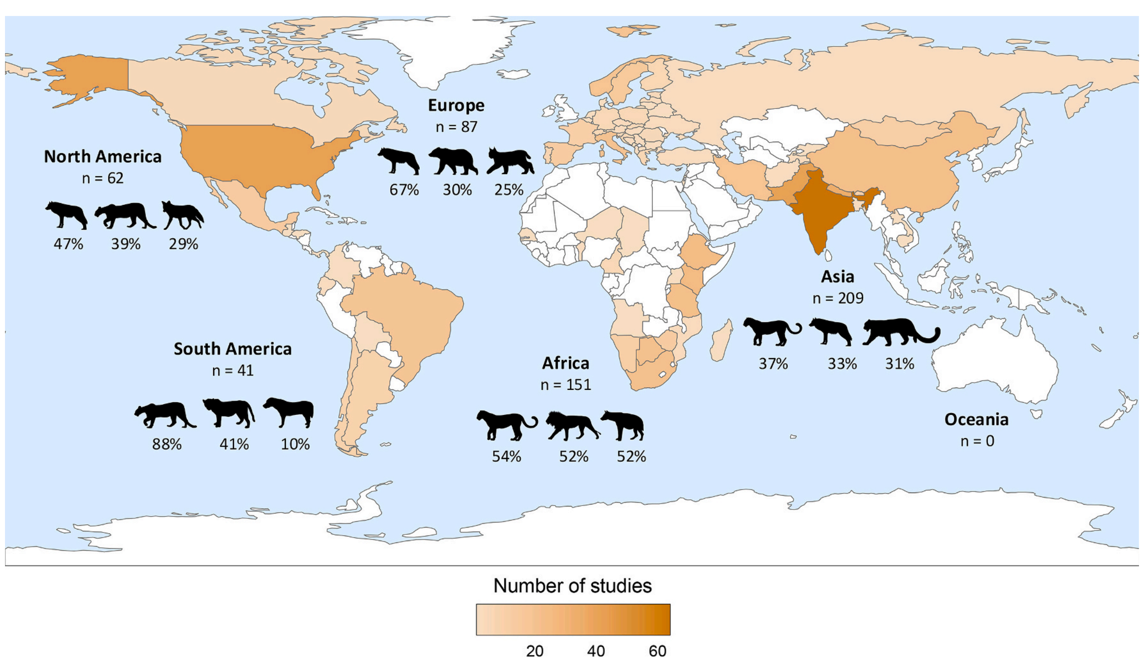

Fig. 4. Map showing all 77 countries in which livestock depredation was investigated, and the number of studies in which they were represented, among 548 reviewed studies of livestock depredation (1997–2025). The representation within the reviewed literature of each continent with livestock is also indicated, as well as each continent's three most studied predator species. Asia: *Panthera pardus* ($n = 78$ of 209, 37 %), *Canis lupus* ($n = 70$ of 209, 33 %), and *Panthera uncia* ($n = 64$ of 209, 31 %). Europe: *Canis lupus* ($n = 58$ of 87, 67 %), *Ursus arctos* ($n = 26$ of 87, 30 %), and *Lynx lynx* ($n = 22$ of 87, 25 %). Africa: *Panthera pardus* ($n = 81$ of 151, 54 %), *Panthera leo* ($n = 79$ of 151, 52 %), and *Crocuta crocuta* ($n = 78$ of 151, 52 %). North America: *Canis lupus* ($n = 29$ of 62, 47 %), *Puma concolor* ($n = 24$ of 62, 39 %), and *Canis latrans* (18 of 62, 29 %). South America: *Puma concolor* ($n = 36$ of 41, 88 %), *Panthera onca* ($n = 17$ of 41, 41 %), and *Canis lupus familiaris* ($n = 4$ of 41, 10 %). Note that more than one country, continent, or predator species can be considered by one study. Additionally, we report predators to species level here, except for *Canis lupus familiaris*, which we chose to separate from *Canis lupus* as we consider dogs and wolves to be too different ecologically and behaviourally to report them together.

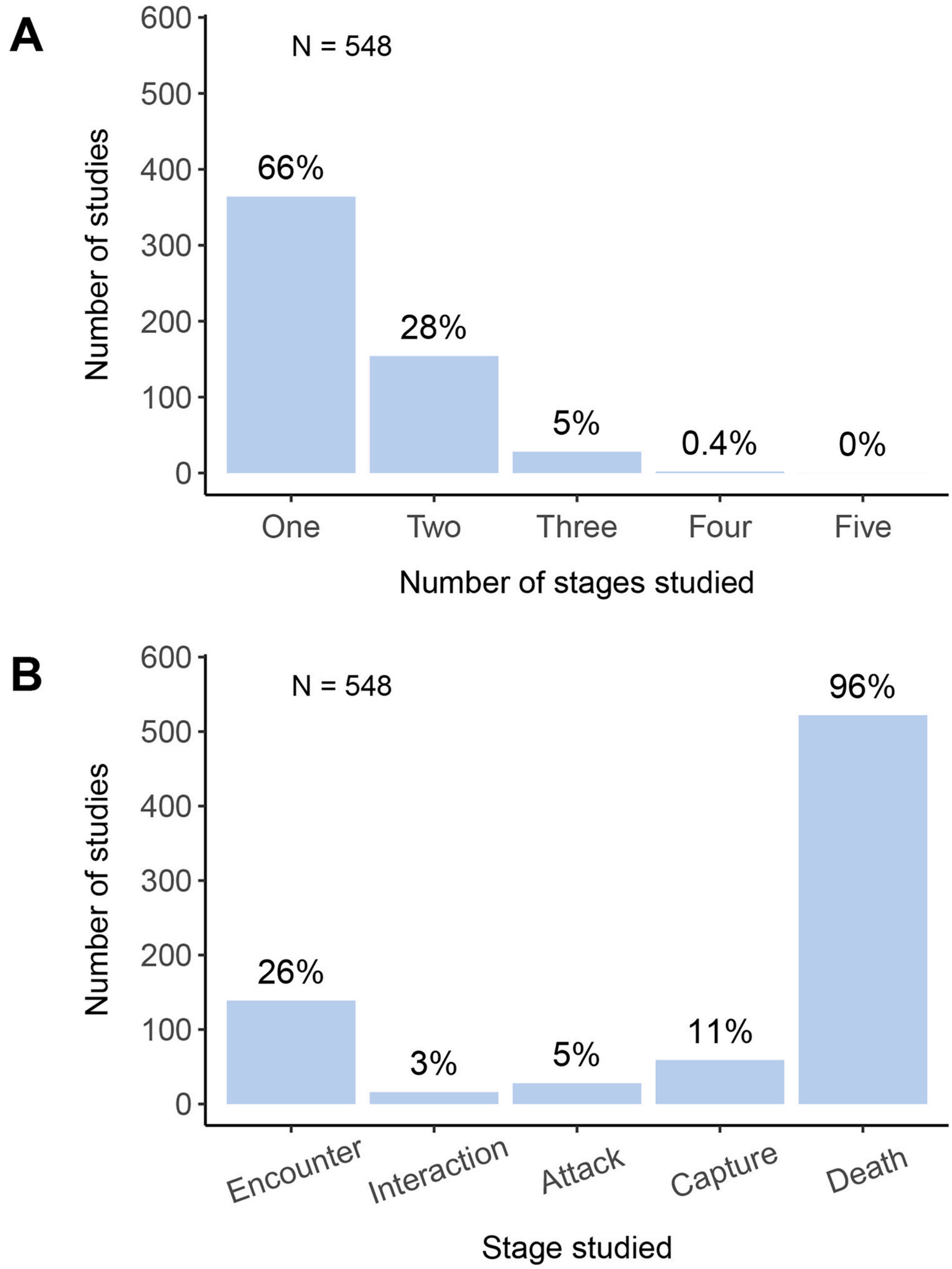

Fig. 5. **(A)** The number of stages of the livestock depredation process that were simultaneously studied by each of 548 reviewed studies of livestock depredation (1997–2025). **(B)** The frequency with which each of the stages was studied among the reviewed literature.

studies, respectively (Fig. 5B; Table 1). In total, only eight studies (1.5 %) made real-time visual observations, either in person or using camera footage, of any stage (Andelt et al., 1999; Atickem et al., 2010; Houser et al., 2011; Zarco-Gonzalez et al., 2012; Macon and Whitesell, 2021; Volski et al., 2021; Hoffmann et al., 2022; Louchouarn and Treves, 2023).

3.2. Methods used to study the stages of the depredation process

The majority of studies examining the *encounter* stage used proxy data to study encounters. For example, 55 % of studies reported the occupancy, distribution, or abundance of either livestock, predators, or both, to infer information about potential encounters ($n = 77$ of 139), and 27 % calculated an index of prey preference based on prey availability ($n = 38$ of 139). Conversely, 4 % of studies of the *encounter* stage made real-time visual observations of encounters using cameras ($n = 5$ of 139; Table 1). Four used the footage to report predator-livestock encounter rates, while one only reported the species seen on the cameras with no indication of frequency. Furthermore, 15 studies (11 %, $n = 15$ of 139) tracked predator movement (Table 1). However, the scale at which predator proximity to livestock was reported varied. Seven of these studies considered encounters in real time by identifying predator presence to within 1 km of specific locations of livestock (i.e., bomas, cattle posts, grazing paddocks, pastures, or collared livestock). Of the other eight, three reported predator proximity to 'households' or 'communities' without making mention of livestock, four evaluated the extent of overlap between predator home ranges and potential livestock locations, and one compared spatiotemporal predator activity data to livestock activity data. Finally, eight studies (6 %, $n = 8$ of 139) tested the effectiveness of interventions targeting the *encounter* stage. These

Table 1
Number and percentage of the 548 reviewed studies of livestock depredation (1997–2025) that studied each stage of the depredation process (as defined in Fig. 2). We also provide the description and frequency of the methods used in the reviewed literature to study each stage. Note that it is possible for one study to consider more than one stage, and to use more than one method to study a stage.

Stage	n (% of total studies)	Method by which the stage was studied	n (% of studies that consider this stage / % of total studies)
Encounter	139 (26 %)	Occupancy, distribution, or abundance estimates of predator and/or livestock	77 (55 % / 14 %)
		Calculation of prey preference based on availability	38 (27 % / 7 %)
		Tracking of predator movement	15 (11 % / 3 %)
		Test of interventions aimed at the *encounter* stage	8 (6 % / 1 %)
		Real-time visual observations of encounters	5 (4 % / 1 %)
		Surveys of predator signs or tracks	3 (2 % / 1 %)
		Computer-simulated encounters	1 (1 % / 0.2 %)
		Records of encounters (e.g., official databases)	1 (1 % / 0.2 %)
		Interviews / questionnaires	1 (1 % / 0.2 %)
		Identification of factors related to potential encounters	1 (1 % / 0.2 %)
Interaction	17 (3 %)	Non-lethal effects of real or simulated interactions on livestock	14 (82 % / 3 %)
		Effects of being seen by livestock on predators	1 (6 % / 0.2 %)
		Computer-simulated interactions	1 (6 % / 0.2 %)
		Tests of interventions aimed at the *interaction* stage	1 (6 % / 0.2 %)
Attack	28 (5 %)	Tests of interventions aimed at the *attack* stage	26 (93 % / 5 %)
		Interviews / questionnaires	1 (4 % / 0.2 %)
		Real-time visual observations	1 (4 % / 0.2 %)
		Computer-simulated attacks	1 (4 % / 0.2 %)
Capture	60 (11 %)	Reporting of numbers of livestock deaths and injuries without distinction	27 (46 % / 5 %)
		Reporting of numbers of livestock deaths and injuries separately	23 (39 % / 4 %)
		Reporting of species-specific bite locations	7 (12 % / 1 %)
		Real-time visual observations	2 (3 % / 0.4 %)
Death	522 (96 %)	Interviews / questionnaires	296 (57 % / 54 %)
		Records of deaths (e.g., official databases)	139 (27 % / 25 %)
		Diet analysis	79 (15 % / 14 %)
		Post-hoc observations of carcasses or depredation sites	72 (14 % / 13 %)
		Real-time visual observations	3 (1 % / 1 %)
		Computer-simulated deaths	3 (1 % / 1 %)
		Use of media reports	1 (0.2 % / 0.2 %)

interventions included chasing or hazing, the use of visual or auditory deterrents, the reduction of anthropogenic waste attractants, and the presence of livestock guarding dogs (the effect of which was tested on predator-livestock encounter rates in one study).

All but three studies that considered the *interaction* stage did so by studying the non-lethal effects of real or simulated interactions with predators on living livestock (82 %, $n = 14$ of 17; Table 1). One study (6 %, $n = 1$ of 17) tested the effectiveness of an intervention aimed at the *interaction* stage, namely the introduction of creole cattle, which have been found to aggressively defend themselves against detected predators, to livestock herds (Valderrama-Vasquez et al., 2024).

Among the studies that considered the *attack* stage, 93 % ($n = 26$ of 28) assessed the effectiveness of interventions aiming to prevent attacks, which were enclosures of various types and fladry (Table 1). One study (4 %, $n = 1$ of 28) made real-time, in-person observations of the *attack* stage, by presenting captive coyotes with lambs (Andelt et al., 1999). This study was also identified as studying the *capture* and *death* stages via real-time visual observations.

Almost half of the studies that considered the *capture* stage (45 %, $n = 27$ of 60) did so by reporting rates of livestock injuries and deaths together, rendering a distinction between the two stages impossible. A further 39 % ($n = 23$ of 60), however, reported injury and death rates separately. Seven studies reported species-specific bite locations (12 %, $n = 7$ of 60), and two studies made real-time visual observations of captures (3 %, $n = 2$ of 60), both of captive carnivores being fed live livestock prey (Andelt et al., 1999; Houser et al., 2011).

The *death* stage was by far the most frequently considered, as it was assessed by 96 % of studies ($n = 522$ of 548). Death rates were reported from various sources (Table 1). Real-time visual observations made up 1 % of these studies ($n = 3$ of 522). Two occurred in captivity (Andelt et al., 1999, Houser et al., 2011), and one at livestock bomas (Atickem et al., 2010).

4. Discussion

While we found that all five stages of the depredation process (Fig. 2) were studied among livestock depredation research (Fig. 5), the vast majority of the literature (96 %) collected or used post-hoc data on the count of livestock killed by carnivores. Such data was used to, for example, report levels of livestock death in different areas, make inferences about the effectiveness of interventions, or predict the intensity of livestock death via biotic and abiotic correlates. In contrast, three of the five stages (*interaction*, *attack*, and *capture*) were studied roughly 10 to 30 times less often than the *death* stage, highlighting an imbalance in depredation research effort. All stages of the depredation process are crucial to predicting predator and livestock behaviour during predatory interactions, and to assessing the probability of livestock death given an encounter with a predator (Miller, 2015; Blackwell et al., 2016; Hoffmann et al., 2022). Thus, our research demonstrates that knowledge gaps persist in livestock depredation research, specifically in reference to the variable behavioural decisions made by predators as they advance through a depredation process, which are integral to designing effective interventions to halt their advance.

4.1. The encounter stage

The *encounter* stage is crucial as the first step of the livestock depredation process (Hoffmann et al., 2022). While distribution data can be used as a proxy to infer potential rates of encounter, this indirect method can be misleading as it equates spatial proximity with the occurrence of an encounter. This may be inaccurate due to the scale at which distribution data is collected, varying detection distances in a given environment, or the willingness of different predators to approach human-dominated areas (Montgomery et al., 2018). Moreover, distribution data does not provide fine-scale information on any patterns in predator approaches of livestock. Real-time data on encounters, whether through visual observation or fine-scale movement tracks, may therefore be important to draw conclusions on the ways in which different predator species navigate the *encounter* stage (Table 2).

Rates of predator-livestock encounters can greatly differ in magnitude from rates of livestock deaths (Hoffmann et al., 2022). Studying the former, especially in combination with subsequent stages such as the *attack* stage, can yield useful information (Table 2). For example, consider two hypothetical species that have, over a period of time, attacked enclosed livestock on an equal number of occasions. Species 1 regularly encountered livestock, but had an attack rate of just 1 %. Species 2 only irregularly encountered livestock, but had an attack rate of 50 %. Although the same number of attacks occurred, the contrasting rates could either reflect different abilities to successfully navigate the encounter-to-attack transition, or reveal important differences in predator behaviour. Species 1 may be encountering livestock while scavenging on discarded livestock carcasses or other waste within human settlements (Abay et al., 2011; Kalyahe et al., 2022). While there, it may opportunistically attack livestock. In this case, interventions such as reinforcing enclosure walls might not reduce encounter rates, which could still engender risk for humans, non-lethal effects on livestock, and continued livestock deaths if the predator finds a way to reach livestock (Scasta et al., 2018). Instead, strategies aiming to decrease the encounter rate itself, such as improved waste disposal methods, may reduce attack rates as a by-product. However, the low encounter rate and relatively high attack rate of Species 2 may indicate a primary motivation to attack livestock. In this case, making enclosure break-ins more difficult for this species could cause the encounter rate to decrease as a by-product. Implementing species-specific, stage-based interventions could lead to more effective mitigation of livestock depredation.

4.2. The interaction stage

In predator-prey ecology, prey can escape in the *interaction* stage following the detection of the predator but before the attack begins. In livestock depredation, prey escape is likely rarer because livestock have lost many anti-predator instincts due to domestication (Geffroy et al., 2020; Beck et al., 2021), and because many depredation attempts occur at night when livestock are often enclosed (Kissui, 2008). However, the *interaction* stage remains important to study given the effects that it can have on livestock, as many livestock within a herd can survive an interaction with a predator. Psychological impacts of interactions can have physiological consequences on livestock with the potential to affect reproduction, foraging, and the quality of derived products such as dairy (Sommers et al., 2010; Cooke et al., 2013). Therefore, financial loss for livestock owners does not only occur as a consequence of predators killing livestock, but can also result from depredation sequences that did not lead to death. Studying the *interaction* stage may reveal ways in which various livestock respond to interactions with predators (Table 2), and thus inform management decisions. Interventions reducing the possibility of livestock detecting predators, such as completely opaque fences, may be useful for livestock that experience negative non-lethal effects of interactions with predators. Alternatively, pastoralists may choose to keep livestock breeds which are found to display more effective anti-predatory behaviours, or which are more effectively able to alert herders to predator presence (Valderrama-Vasquez et al., 2024; Table 2).

4.3. The attack stage

The way in which the *attack* stage is navigated can vary between predator species due to innate biological differences in predatory behaviour. In the context of livestock depredation, the added human dimension may lead to further differences. For example, enclosure walls may deter some predators more than others. They may also be breached using different strategies. Spotted hyenas have been found to reach livestock by pushing through fences or digging, while leopards can scale

Table 2
Proposed methods and research questions with which to study all stages of the livestock depredation process, with the aim of unifying livestock depredation research with predator-prey ecology.

Proposed method	Targeted stage	Data to collect	Example research questions
Use of camera traps or other visual recording devices	Encounter	Predator-livestock encounter rates	Which predator species encounter livestock in a given area, and how frequently do they do so?
		Temporal and spatial data on encounters	When do predators encounter livestock most? From which direction do predators approach livestock?
		Predator behaviour	Which predatory behaviours do predators display when approaching livestock?
	Interaction	Livestock behaviour	How quickly do different types of livestock notice predator presence when enclosed or free-ranging? Which behaviours do livestock display when predator presence is detected?
	Attack	Attack rates	Which predator species attack livestock (e.g., breach enclosure barriers) in a given area, and how frequently do they do so? How likely are different predator species to attack livestock once an encounter has occurred?
		Predator behaviour	How do different predator species breach enclosure barriers?
	Capture	Predator behaviour	Do capture strategies differ based on the number of livestock present, livestock species and breed, the size of enclosures, or whether livestock are enclosed or free-ranging?
Use of GPS collars / accelero-meters on predators	Encounter	Long-range movement tracks	Do predators make targeted journeys to livestock locations, or do they make opportunistic visits to livestock during other types of journeys?
		Short-range movement tracks	Do predators display exploratory behaviours such as circling around a livestock enclosure before attacking?
	Attack	Predator behaviour	Which fine-scale movement patterns do predators display when attacking livestock (e.g., body posture, tri-axial movement, speed)?
Periodic surveys of predator tracks	Encounter	Predator-livestock encounter rates	Which predator species encounter livestock in a given area, and how frequently do they do so? *Track surveys are a low-cost alternative to cameras. Predator tracks can be detected using passive survey techniques (observation only) or active survey techniques (e.g., creating mud plots or*

(continued on next page)

Table 2 (*continued*)

Proposed method	Targeted stage	Data to collect	Example research questions
			sand plots around livestock enclosures or grazing areas).
Experiments using dummy livestock	Encounter	Predator behaviour	Do approach strategies differ when livestock occur in different numbers, densities, configurations, and are of different species or breeds? *Dummy livestock may be a useful experimental method to answer research questions by manipulating conditions, provided that predators perceive them to be live prey. Additionally, data could be obtained more quickly by attracting carnivores to dummy livestock locations using call-ups, rather than waiting to collect data on sporadic attacks of real livestock.*
	Attack	Predator behaviour	Do attack (e.g., barrier-breaching) strategies differ when livestock occur in enclosures in different numbers, densities, configurations, or are of different species or breeds?
Recording of audio	Encounter	Association of auditory stimulus with predator movement	Do stochastic noises (e.g., baby crying, humans talking, etc) made in proximity to livestock enclosures have any effect on the movement and actions of approaching predators? *To answer this question, audio recordings should be used alongside GPS collars or cameras.*
	Interaction	Association of predator presence with livestock alarm calls	Are certain species or breeds of livestock more reactive, via alarm vocalisations, to predator presence than others? Does livestock alarm cause predators to change their behaviour? *To answer these questions, audio recordings should be used alongside cameras or GPS collars.*
Use of heartrate monitors	Interaction	Association of predator presence with livestock stress levels	How are the stress levels of different species or breeds of livestock affected by predator approaches, presence, and attacks? *To answer this question, heartrate monitors should be used alongside cameras or GPS collars.*
Playback experiments	Interaction	Livestock reactions to simulated predator presence	How are livestock reactions and/or measurable stress levels affected by simulated predator presence via the playback of predator sounds? *To answer this question, playback experiments should be used alongside cameras, visual observations, heartrate monitors, and/or audio recordings.*
Surveys of injured or dead livestock	Capture	Rates of livestock injuries	How often are livestock injured by different predator species in a given area? How do injury-to-death ratios compare between predator species or management scenarios?
	Death	Rates of livestock deaths	How often are livestock killed by different predator species in a given area?

fenceposts or jump (Kolowski and Holekamp, 2006). Fence types that are difficult to push through may be easier to climb, while those that are harder to scale may not withstand blunt force. Thus, the use of different fence materials in livestock corrals can, depending on their properties, prevent one species from breaching the barrier while facilitating entry to another. Knowledge of species-specific behaviours at this stage can drive the choice of the most effective intervention in a given area, based on which species are most problematic. Wherever possible, collecting data on predator behaviour during the *attack* stage would be facilitated by studying the stage in real time, via varied methods such as visual recording devices, accelerometers, or even staged attacks using dummy livestock (Table 2). Post-hoc inferences can provide information on whether given interventions are successful or not, but relating these successes or failures to specific observed behaviours would greatly increase predictive power over depredation events.

4.4. *The capture stage*

Prey capture does not always lead to death. In the case of depredation, livestock injury can represent a substantial proportion of the reported effects of predator attacks (Woodroffe et al., 2005; Braczkowski et al., 2020; Tarimo et al., 2021). Our review indicates that there are more studies reporting rates of livestock injury and death together than studies reporting them separately. Though the former type of study does consider instances of non-lethal injury, no information specifically relating to the capture stage can be inferred, which represents a missed opportunity. Frequency of injury may vary with factors such as predator species, whether livestock were enclosed, or herd size. Knowing whether certain predator species have higher tendencies towards surplus injuring or killing under various management scenarios could be valuable information (Thapa, 2021). Finally, it may be useful to know whether capture strategies of various predators differ with varying conditions such as livestock type, density, and whether livestock are enclosed or free-ranging (Table 2).

4.5. *The death stage*

Collecting data at the *death* stage has helped inform management actions and provided indications of where to focus interventions (Miller, 2015). The limited resources required to collect this data and the potential management impact likely explain the overwhelming focus of depredation research on this stage. However, using only data on livestock death can be misleading, especially when associating levels of death with risk of depredation. Depending on the predator species, a low death rate does not equal a low encounter rate, as discussed above. High encounter rates with relatively low death rates can occur due to the presence of interventions, or differences in predator willingness or ability to attack livestock after an encounter. A low risk calculated using only death data might increase if local herding practices or management strategies are changed, and would thus not be a reliable indicator of true risk. Moreover, unsuccessful attacks, or even simply encounters, may still impact livestock fitness and human safety (Dickman et al., 2014; Singh et al., 2015; Widman et al., 2019). Additionally, studying the *death* stage alone provides limited information on the events leading to death. In bypassing the first four stages of livestock depredation, understanding of the spectrum of depredatory behaviours displayed between and within predator species will remain limited.

Although death is presented by Lima and Dill (1990) and this study as the final stage in the predation process, it may also be useful within the context of livestock depredation to consider consumption as a potential stage succeeding death. While the occurrence of consumption does not change the outcome of a predation event for the prey, rates of consumption of livestock kills could yield useful information if measured in relation to, for example, the recurrence of depredation by individual predators, rates of death, or wild prey availability. Though some studies do report consumption rates in addition to death rates (e.g., Weise et al., 2020), we note that this is not currently a commonly explored avenue of research.

4.6. General discussion

Our findings indicate that integration of predator-prey theory into depredation research is lacking, despite calls by a handful of recent studies for a shift in that direction (Blackwell et al., 2016; Haswell et al., 2019; Wilkinson et al., 2020; Hoffmann et al., 2022). We have identified various methods of research that could be used to study the successive stages forming the livestock depredation process, of which examples can be found in Table 2. These methods have the potential to answer novel research questions, and in doing so provide insight into the behaviours of both predators and livestock during their interactions, with relevance to management and conservation (Table 2). If more is known about how different predator species are expected to act when pursuing livestock, and how livestock are expected to react to predators, an evidence-based approach to developing interventions will become possible. These interventions will then be adaptable depending on area-specific conditions such as the identity of the most conflict-causing predator species, the type of livestock kept, or specific needs of livestock owners.

We recognise that studying depredation in a way that separates it into distinct, observable stages can require time and resources, depending on the methods used (Table 2). Though livestock depredation is a global phenomenon (Fig. 4), seven of the top ten countries represented in this review (Table S2) are classified as having low-income or lower-middle-income economies (The World Bank Group, 2024). It is unrealistic to expect a completely equitable distribution of empirical research effort between the five stages of depredation, if some require more time and technological resources to study than others. However, some low-cost methods, such as periodic predator track surveys around livestock enclosures or grazing areas (Table 2), can be used to study some of these stages. Moreover, in cases where a fundamental shift in research methods is not possible, we recommend that any results obtained (such as levels of livestock injury and death) be reported in such ways that behavioural differences can be derived between predator species. This would still contribute to building a database on species-specific behaviours in these stages. We also encourage conservation organisations to incentivise ecologically-focused research as it shows promise for the long-term success of interventions to reduce depredation rates. Tailoring interventions to different stages and predator species will promote more effective conservation action for the sake of local people, livestock, and carnivores.

CRediT authorship contribution statement

Anna Rouviere: Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Conceptualization. **Robert A. Montgomery:** Writing – review & editing, Supervision, Conceptualization.

Declaration of competing interest

The authors confirm they have no conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2025.111330.

Data availability

The data collected from all 548 studies included in this review, and tables listing all predator taxa and countries considered among these studies, can be found in the Supplementary Material.

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