Coexistence, Competition, and Contradiction: Synthesizing Recent Evidence on Wildlife-Livestock Relationships in East Africa

by

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Abstract

East African rangeland ecosystems are globally renowned biodiversity hotspots. They have also sustained humans and livestock for millennia. Prior research has shown that wildlife and livestock of similar guilds compete for resources, potentially threatening some wild species. This conclusion has shaped many conservation policies, restricting pastoralist and livestock access to protected areas (PAs) and resulting in many conflicts. However, newer research at finer scales suggests that the nature of wildlife-livestock relationships is more nuanced. However, this evidence has yet to be systematically reviewed and contextualized to offer prescriptive advice for researchers and policymakers moving forward.

Our review addresses this gap by exploring four decades of empirical ecological research on the wildlife-livestock relationship in this region. We asked: 1) What methods and evidence have ecologists used to characterize the relationships between wildlife and livestock in East African rangelands? 2) What conclusions have they reached about the nature of the relationship? We created Sankey diagrams to visually map the relationships between methodologies, evidence, and the conclusions that go on to inform policy. Our review revealed a wealth of diverse evidence from East Africa, including both positive and negative responses from wildlife and livestock. We find that evidence based on spatial overlap is prone to inconsistent interpretation and can benefit from a more rigorous application of ecological concepts. Most conclusions are neutral, which challenges policies that assume competition between wild and domestic herbivores. We also find that most positive evidence is linked to land use and livestock management conditions. These insights hold implications for policymakers, pastoralist communities, and researchers seeking sustainable solutions in East Africa's socially and ecologically complex environments.

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Thank you,
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1. Introduction

Visitors driving through many of East Africa's protected areas (PAs) today will encounter iconic wildlife, such as zebras, elephants, giraffes, and wildebeest. They are, however, unlikely to encounter cattle or people (Garland, 2008). While the perceived absence[1] of people and livestock may be taken for granted by many visitors, it is a relatively new phenomenon given the historical presence of pastoralism and mobile grazing cultures that emerged in dryland East Africa approximately 4,000 years ago, significantly influencing its rangeland ecology (Lankester & Davis, 2016). In the nineteenth and twentieth centuries, pastoralism was linked to overgrazing and environmental degradation; PAs were established to protect nature by excluding people and livestock (Collett, 1987; Garland, 2008; Dowie, 2011; Boles et al., 2019). These restrictive conservation policies led to decades of debate and conflict, with different viewpoints on the compatibility of wildlife and livestock boiling over "into anger and entrenched positions" (Niamir-Fuller et al., 2012, 8). Despite these entrenched positions, the actual nature of the wildlife-livestock relationship is a subject of empirical uncertainty (Niamir-Fuller et al., 2012; Pozo et al., 2021).

Research suggesting that livestock compete with wildlife for limited resources is prevalent in the ecological literature (Prins, 1992; Voeten & Prins, 1999; Schieltz & Rubenstein, 2016). This has contributed to a perception that competition between wildlife and livestock is a given, prompting many authors to begin their manuscripts with a statement of competition as a matter of fact (Box 1). However, the extent to which livestock and herbivorous wildlife actually compete in rangelands remains a matter of contention (Butt & Turner, 2012; Pozo et al., 2021). Some of this uncertainty is rooted in methodological limitations or conceptual vagueness. For example, many studies on competition deploy methods that only measure short-term responses to resource availability despite the large resource variations typically characterizing rangeland ecosystems (Schieltz & Rubenstein, 2016). Additionally, the concept of ecological competition has itself required clarification (Butt & Turner, 2012). According to Prins' (2000) definition, competition requires three conditions: (1) populations of two species must share a resource; (2) the resource must be limited; and (3) one species must negatively affect resource availability for the other species. However, as Butt & Turner (2012) have observed, many studies used inconsistent definitions to measure and prove competition.

Adding to the confusion, evidence also suggests that livestock and wildlife may not compete at all, but have facilitative relationships depending on contexts (Young et al., 2018). Facilitation

[1] People are, of course, not truly absent from these landscapes. Indigenous peoples have often been evicted but traverse the landscape in hidden or concealed ways. Tourists and the network of staff that support them are also visible, and in significant densities in some places.

refers to a positive interaction in which one species indirectly benefits the other by enhancing resource availability. For example, Odadi et al. (2011a, 2011b) suggest that facilitation can occur when a species stimulates the growth of quality forage or clears undesirable vegetation, benefiting a second species. Positive relationships, like facilitation, may depend on favorable circumstances, including range management techniques or climate conditions (Young et al., 2005; Western et al., 2020). In rangelands with alternating rainy and dry seasons, multiple studies show evidence of competition during dry periods, whereas facilitation emerges in wet periods (Bhola et al., 2012; Odadi et al., 2011a). Most scholars agree that wildlife and livestock in dryland systems influence each other through shared resource use, whether that use is characterized by facilitation or competition.

Box 1. *Perception of wildlife-livestock competition in the scholarly literature.*[2]

"The most enduring public images of extensive rangelands are of pasture land overgrazed by livestock, and therefore in environmental crisis, and threatening wildlife and biodiversity" (Niamir-Fuller et al., 2012, 2).

"Wildlife is viewed across many savannah rangelands as directly competing for forage resources with livestock, and often livestock is blamed for the large declines in wildlife…management decisions are often based on this assumption, with livestock excluded for the benefit of wildlife" (Tyrrell et al., 2017, 60).

"The assumption that biodiversity is higher in protected areas than in other land uses has dominated biodiversity conservation discourse" (*First sentence,* Nyamukuru, 2019, 124).

"Competition between wildlife and pastoralist livestock over access to rangeland habitat has become an important conservation challenge in the 21st century" (*First sentence,* Masiaine et al., 2021, 1).

"Livestock encroachment is threatening the populations of large wild mammals in Tanzania. Competition for quality grazing land by domestic stocks is one of the main factors impacting wild species during this encroachment." (*First sentences,* Bonnington et al., 2007, 658).

"Global concerns on the competitive effects of livestock on wildlife have increased in a variety of ecosystems" (*First paragraph,* Sitters, 2009, 738).

"Livestock grazing is an increasing conservation challenge throughout protected wildlife areas in Africa" (*First sentence,* Atickem and Loe, 2014, 343).

[2] Similar sentiments are present in non-academic literature, e.g., Kenya: 400,000 Cattle Invade Game Park: "At least 400,000 head of cattle have invaded the Tsavo West National Park, depriving wildlife of pasture and water" (Ringa, 2015).

Beginning in the 1980s, researchers challenged the view that resource limitation primarily governs the livestock-wildlife relationship, particularly in "non-equilibrium" ecosystems, or environments that experience high variability and disturbance (Vetter, 2005; Niamir-Fuller et al., 2012). This research was a radical shift from equilibria ecology, which previously governed many understandings of animals and their interactions with the environment (Zimmerer, 2000). Non-equilibrium ecology emphasizes that factors other than wildlife density-dependent vegetation changes influence ecosystem dynamics (Illius and O'Connor., 1999; Vetter, 2005). Within dryland East Africa, drought, hunting, and land use change are thought to be more responsible for the wildlife declines than competition with livestock (Ottichilo et al. 2000a; Ottichilo et al. 2000b; Georgiadis et al., 2007a; Georgiadis et al., 2007b).

Given this uncertainty, systematic reviews of the wildlife-livestock relationship are needed to aggregate the current state of knowledge to inform current research, policy, and practice (Bayliss et al., 2016). Systematic reviews also allow researchers to identify inconsistencies across methodologies, concepts, or interpretations of the evidence (Chaikina & Ruckstuhl, 2006; Schieltz & Rubenstein, 2016). For example, Schieltz and Rubenstein's (2016) global review investigated the impact of livestock on a broad array of wildlife and found evidence that largely supports a negative relationship between the two. However, this conclusion predominantly relied on studies from North America and Europe with considerable variations in methodology and quality (Schieltz & Rubenstein, 2016). In East Africa's rangelands, on the other hand, people have kept livestock for millennia (Lankester & Davis, 2016). The relatively long co-evolutionary history between livestock and ungulates of similar guilds may produce evidence that differs from North America and Europe; indeed, Schieltz and Rubenstein's (2016) global review suggests a positive relationship when isolating evidence from Africa.

East Africa also emerges as a region worthy of review due to its social-ecological complexities, including a high density and distribution of wildlife, the historical presence of pastoralism, and the large role that wildlife tourism plays in national economies. Since the twentieth century, East Africa has been home to some of the world's most iconic rangeland PAs, including the Masai Mara National Reserve (MMNR) in Kenya and Serengeti National Park in Tanzania. These parks are considered refuges for a global biodiversity heritage. The separation of wildlife and livestock in these areas has generated violent conflicts (Infield et al., 2008; Dowie, 2011; Mbaria & Ogada, 2016; Masiaine et al., 2021). As a result, research on the wildlife-livestock relationship has sustained passionate academic and political debates, resulting in the "entrenched" research positions and anger observed by Niamir-Fuller et al. (2012, 8).

With this brief background, and to advance research to action, our research objective is to conduct a systematic review of the evidence on wildlife-livestock relationships in East Africa, concentrating on the responses of wildlife and livestock across similar guilds.

2. Methods

2.1. Research Questions

Given our research objective, we ask the following questions:

1. What methods and evidence have ecological researchers used to characterize the relationships between wildlife and livestock in East African rangelands?
2. What conclusions have they reached about the nature of the relationship?

We visually link methods, evidence, and study conclusions together in a graphical representation known as a Sankey diagram to clarify sources of uncertainty and to understand how and why evidence coalesces into conclusions. This illustrates the flow of information that contributes to current and heated debates on rangeland management and conservation policy and illustrates relationships within and across the included studies.

2.2. Search Criteria and Selection Strategy

We used the Clarivate Web of Science database (Clarivate, n.d.) to identify relevant studies for our review. In addition, we read key reference papers to situate ourselves in the current state of ecological research on the wildlife-livestock relationship, as well as related policy and management debates. A list of these reference papers is included in Appendix I.

We used the following search terms in February 2023 to capture relevant articles: *TS = ((wildlife OR herbivore OR ungulate) AND (livestock OR cattle OR cow) AND (relationship OR competition OR compensation OR facilitation OR displacement) AND ("East Africa" OR Kenya OR Tanzania OR Serengeti OR Mara)) AND PY=(1980-2023).* We chose to begin our review in 1980 to capture the last four decades of ecological research, which encompasses the debates over the influence of climate in non-equilibrium rangeland ecosystems, like those found in East Africa (Lamprey & Reid, 2004).

This initial search yielded 158 studies that matched our query criteria. To meet our research objectives, we narrowed our selection to studies that only met the following criteria:

1. Geographic: Rangelands and savannah ecosystems of East Africa, including any ecosystem where livestock would potentially graze. Our selection thus included studies from eligible landscapes in Zimbabwe and Ethiopia, countries that are not ordinarily categorized as “East Africa.”
2. Livestock: Domestic herbivores, including cattle, camels, sheep, goats, and donkeys.
3. Wildlife: Herbivorous mammals, including grazers and browsers.

4. Methods and results: Generated original empirical data, or drew upon existing empirical data, to produce evidence and generate conclusions about the wildlife-livestock relationship.

Because our research aims to understand the relationship between livestock and wild ungulates of similar guilds, we excluded studies that focused on interactions between livestock and carnivores, insects, or small mammals.

We conducted the initial screening of titles and abstracts to identify relevant articles. We obtained full-text articles for further evaluation if their eligibility was unclear from the title and abstract. This yielded a total of 46 papers from the original 158 for our systematic review.

2.3. Data Extraction

Data were independently extracted by at least two authors. The following data were initially extracted from each included study:

Table 1. *Data extracted from studies.*

Data	Description
Study characteristics	Author, journal, publication year, study location.
Methods type	Standardized into the following categories: Camera traps and continuous recordings, experimental plots, transects, interviews, population surveys, telemetry tracking, remote sensing, mixed methods, and others.
Methods scale, variables, and measurements	Descriptions of measurements, specific variables of interest, species identified, spatial scale of study location, duration of study.
Summary of key findings	Description of the study's key findings and takeaway message on the wildlife-livestock relationship.
Evidence for competition or a negative relationship	Description of the study's results, or empirical evidence for a competitive or negative relationship between wildlife and livestock.
Evidence for facilitation or a positive relationship	Description of the study's results, or empirical evidence for a facilitative or positive

	relationship between wildlife and livestock.

2.4. Data Synthesis

(i) Synthesizing evidence: To identify patterns in the evidence within and across studies, we standardized and grouped evidence by type (see Popay et al., 2006). By relying on the authors' descriptions of their methods and results, we identified 11 distinct types of evidence that are commonly used to explain the wildlife-livestock relationship. We did this for two reasons: 1) to understand the most common mechanisms researchers have used to describe and understand the wildlife-livestock relationship, and 2) to identify whether the same type of evidence, such as spatial overlap, is interpreted inconsistently.

We then grouped all evidence by value statements: positive, negative, or neutral. This allowed us to identify whether types of evidence were prone to inconsistent interpretations. We derived value statements by analyzing the study authors' interpretations of their evidence. Specifically, we analyzed how authors explained and contextualized their evidence and its implications for the wildlife-livestock relationship. Table 2 outlines the evidence types, descriptions, and examples of interpretations in this study. To minimize individual subjectivity in interpretation, each paper was read at least three times by two people. We compared and discussed notes and findings to ensure consistency across the data synthesis process.

Table 2. *Synthesis of evidence types used by authors in our review to make inferences about the wildlife-livestock relationship.*

Type of evidence	Description	Example of positive interpretation	Example of neutral interpretation	Example of negative interpretation
Spatial overlap	Spatial dynamics of animal presence on the land relative to other species. Keywords include "overlap," "co-occurrence" or "co-existence."	Impala, giraffe, and two species of gazelle benefit from short grass on livestock ranches (Ogutu et al., 2014).	Grevy's zebra spatially overlap with livestock, but it is unclear whether this results in competition (Low et al., 2009).	Wildebeest, cattle and zebra show overlap in space, indicating strong potential for competition (Voeten & Prins, 1999).

Spatial non-overlap	Spatial dynamics of animal absence on the land relative to other species. Keywords include "displacement," "exclusion," "avoidance," and "segregation."	*No positive example from our systematic review.*	Wild grazers and cattle separate to partition water resources as a coexistence strategy (Sitters et al., 2009).	Wildebeests avoid the edges of PAs, where pastoralist settlements and livestock are located (Veldhuis et al., 2019).
Habitat use	Whether and how wildlife and livestock utilize the same landscape differently.	*No positive example from our systematic review.*	*No neutral example from our systematic review.*	Eland habitat use is reduced by the presence of cattle, across seasons and cattle stocking density (Wells et al., 2022).
Abundance correlation	Counts and comparisons of wildlife and livestock within a bounded area or areas.	Wild species dung counts are higher on ranches than within an adjacent PA, suggesting ranches support higher wildlife abundance (Nyamukuru, 2019).	Aerial surveys reveal a significant increase in cattle abundance, but contrary to the hypothesis, no decline in abundance for any wildlife species (Gandiwa et al., 2013).	Dung counts support a theory that an absence of cattle correlates with an increase in zebra (Young et al., 2005).
Richness correlation	Comparisons of species richness within a bounded area or areas.	Species richness is 53% higher in planned vs. unplanned cattle grazing plots (Odadi et al., 2017).	Species richness is highest in a PA, intermediate in a mixed-use grazing and conservation area, and lowest in a settled area (Kiffner et al., 2020).	Domestic herbivore numbers are negatively correlated with resident and migratory herbivore species richness (Green et al., 2019).

Forage conditions	Aspects of forage quality or quantity.	Integrated wildlife-livestock properties had higher forage quality than either wildlife or livestock properties (Keesing et al., 2018).	In the dry season, canopy cover is the most important factor influencing wildlife distribution (Mworia et al., 2008).	A strong reduction in maxNDVI corresponds with areas traversed by pastoralists and livestock (Veldhuis et al., 2019).
Animal behavior	Aspects of behavior, such as bite rate or step rate.	Reducing cattle stocking density can benefit cattle foraging efficiency, measured by step frequency (Wells et al., 2022).	Elephants adjust their habits, becoming more nocturnal, when sharing forage and water resources with pastoralists (Duporge et al., 2022).	Decreased bite rates and increased step rates indicate cattle forage less efficiently on shared grazing plots with wildlife in the dry season (Odadi et al., 2009).
Demography and fitness	Aspects of physical performance, such as weight gain, or population dynamics, such as birth rates or recruitment.	Cattle gain weight under planned grazing schemes (Odadi et al., 2017).	*No neutral example from our systematic review.*	Cattle experience depressed weight gain when sharing forage areas with wild herbivores in the dry season (Odadi et al., 2011a).
Disease dynamics	Transmission and prevalence of diseases shared between wild animal populations and domesticated livestock.	The presence of insecticide-treated cattle can reduce overall tick abundance, potentially benefiting wildlife health (Keesing et al.,	*No neutral example from our systematic review.*	Malignant catarrhal fever passes from wildebeest to cattle, forcing pastoralists away from prime grazing in the wet season

		2018).		(Bedelian et al., 2007).
Predation risk	Benefits and risks of proximity to wildlife or livestock in deterring or attracting predators.	Small herbivores benefit from better visibility on Maasai pastoral ranches (Bhola et al., 2012).	Converting a livestock ranch to wildlife tourism encouraged predators, which resulted in herbivore declines (Georgiadis et al., 2007b).	*No negative example from our systematic review.*
Predictive	Mathematical inferences on the future compatibility of livestock and wildlife based on existing data sets, for example wildlife, human and livestock biomass and energy requirements.	*No positive example from our systematic review.*	*No neutral example from our systematic review.*	A 4% population growth rate in the Ngorongoro District will result in urbanization of the area by 2027 (Prins, 1992).

(ii) Synthesizing conditional factors: Conditional factors, such as seasonal climatic variations or livestock management techniques, can significantly alter evidence and responses (Bhola et al. 2012; Riginos et al., 2012; Young et al., 2018). We therefore noted when the authors presented evidence predicated on conditional factors, or when authors added qualifiers to their evidence to acknowledge these conditions. Similarly, evidence may be qualified when different species exhibit different responses, or individuals of the same species in a population exhibit different responses. We identified the following conditional factors that affected evidence in our review:

- **Management:** Positive or negative evidence was conditional to rangeland management practices or policies. For example, this could include rotational grazing techniques or cattle stocking density.
- **Seasonal:** Evidence varied across seasons. For example, in regions with rainy and dry seasons, evidence may appear positive in one season but negative in another. This

highlights the importance of considering seasonal variations in research conclusions about the wildlife-livestock relationship.

- **Species:** Responses varied across species, resulting in evidence that could appear positive for one species but negative for another.
- **Population:** Responses varied within a population, resulting in evidence that could appear positive for one class or subgroup within a population but negative for another.

A full table of evidence, conditions, and interpretations derived from each study in our review is available in Appendix II.

(iii) Synthesizing conclusions: Finally, we organized studies according to their overall conclusion on the wildlife-livestock relationship. This step sought to understand the entrenched positions noted by Niamir-Fuller et al. (2012) on wildlife and pastoralism, as well as Boles et al.'s (2019) observation that "academic theorising" has historically vilified East African pastoralists (Boles et al., 2019, 419). Our goal was to identify inconsistencies between evidence and research conclusions that could indicate the impact of subjective, entrenched narratives or theories on the wildlife-livestock relationship. We employed a thematic analysis methodology for this step (see Clarke & Braun, 2017). Thematic analysis is a qualitative method that aims to move beyond data summary by identifying and interpreting key aspects of the data, including patterns of meaning (Clarke & Braun, 2017).

To complete this step, two authors read each study to analyze its holistic impact and take-away message, from the abstract to the conclusion. We paid attention to word choice in the studies that may reveal bias, such as using the terms "invasive," "alien," or "exotic" to describe livestock (Larson, 2008). We noted if the authors discussed variations or conditions in their results in equal detail. We also noted if authors contextualized their results within current debates on the wildlife-livestock relationship, which could serve to advance either a positive or negative narrative.

Table 3 describes how we synthesized the conclusions of each study.

Table 3. *Synthesis of conclusions drawn by authors in our systematic review.*

Conclusion	Definition
Positive	Studies with evidence that is interpreted to support a conclusion of facilitation or coexistence between wildlife and livestock.
Negative	Studies with evidence that is interpreted to support a conclusion of competition, or

	negative impacts, between wildlife and livestock.
Conditional Positive	Studies with findings that are interpreted to suggest a beneficial relationship under specific conditions or contexts.
Conditional Negative	Studies with findings that are interpreted to suggest a negative relationship under specific conditions or contexts.
Neutral	Studies with findings that do not strongly support either a positive or negative relationship or provide inconclusive results.

2.5. Visualizing Synthesis in a Sankey Diagram

We created a Sankey diagram to provide a representation of linkages between study methods, evidence, interpretations, conditions, and conclusions. A Sankey diagram is a graphical illustration of complex information flows, in which the width of arrows is proportional to the quantity of information it represents (Nuttbohm et al., 2009). Sankey diagrams have been used to represent systematic review findings in the fields of epidemiology and medicine (Glover et al., 2022; Yang et. al, 2022). We chose this type of diagram to illustrate the relationships between components of our data extraction and data synthesis processes and to visually identify patterns across different studies' methodologies, evidence types, and conclusions.

2.6. Limitations

We recognize that within the limitations of a published article, researchers must distill complex and sometimes fraught ideas into a tight economy of words, tables, and figures. In the thematic analysis step (see Section 2.4), we also recognized the risk of inserting our biased interpretations of the authors' words and conclusions. To reduce this risk, two authors independently read each study three times. Despite these limitations, we opted to complete a thematic analysis due to its effectiveness in examining patterns of social meaning related to empirical data (Clarke & Braun, 2017). Further, study conclusions play a crucial role in informing perception about the wildlife-livestock relationship. When analyzed as a component of a thorough systematic review, this analysis bridges evidence and perception, both of which inform policy and practice (Siddaway et al., 2019).

3. Results and Discussion

Our systematic review of 46 empirical studies synthesizes and analyzes four decades of knowledge on the wildlife-livestock relationship in East Africa.

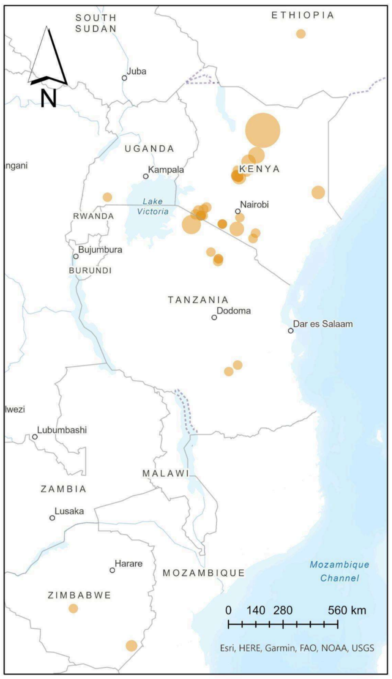

Figure 1. *Map representing the location and spatial scale of the studies in our systematic review. The color saturation of the bubbles represents the concentration of studies in that area, with darker saturation indicating overlapping studies. The size of the bubbles indicates the spatial scale of the studies.*

Most studies originated in Kenya (n = 36), particularly the rangelands of north-central Kenya (n = 16; Figure 1). Eight studies collected data at Mpala Research Centre, a 194 km^2 "living laboratory" and experimental research site in Laikipia County (Mpala, n.d.). This was more than any other single location. Among the studies that have sufficient information to determine scale (n = 44), the average spatial scale was 7,477.18 km^2 (standard deviation = 17,631.5 km^2).

Most studies investigated cattle (typically *Bos taurus* and/or *Bos indicus*) along with other types of livestock, mainly sheep (*Ovis aries*) and goats (*Capra aegagrus hircus*) but also camels and donkeys (Table 4). Three studies did not specify livestock species and instead collected data on variables associated with livestock, such as measuring wildlife distance from bomas (corrals) as a proxy for livestock (e.g., Duporge et al., 2022).

Table 4. *Livestock species of interest.*

Livestock species of interest	Number of studies
General livestock, including cattle, sheep, goats, camels, donkeys, and pigs	24
Cattle only	18
Proxy variables (e.g., boma locations)	3
Camels only	1
Sheep and goats only	0

Below we summarize key takeaways from our research.

3.1. Coarse-scale methods are dominant in current research

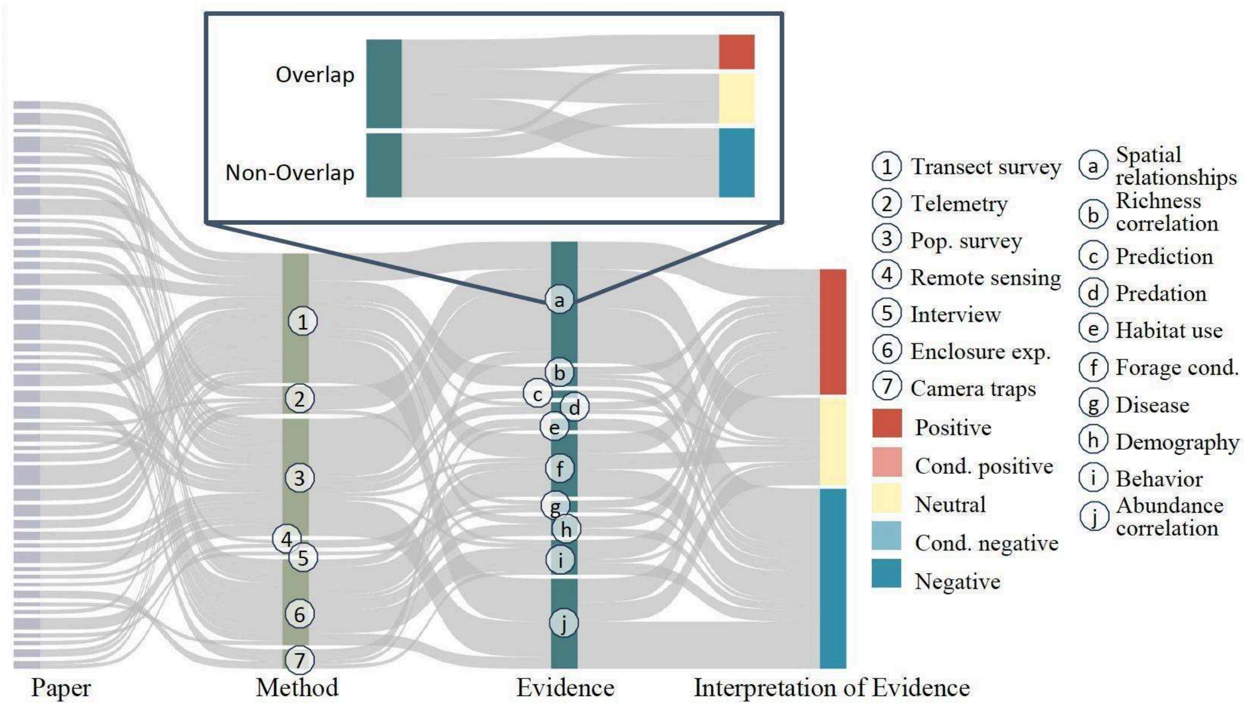

Figure 2. *The Sankey diagram illustrates the 100 lines of evidence produced by the papers in our systematic review. The evidence flows through groupings according to methodology, evidence type (see Table 2), and the author's interpretation of the evidence as either positive, negative, or neutral.*

Figure 2 shows that the most common methods were population surveys (n = 18) and transect surveys (n = 14). Population surveys included both aerial censuses (n = 12) and ground censuses (n = 6). Transect surveys involved recording animal occurrences or sampling forage along linear paths.

Population estimates through several types of surveys were used to assess animal abundance and distribution at broad spatial and temporal scales. Study areas were large, ranging from 1,530 km^2 to 20,057 km^2. Aerial survey datasets from state agencies or wildlife monitoring programs were commonly used, allowing researchers to investigate long-term trends over years or decades. For example, five studies analyzed data from Kenya's Directorate of Resource Surveys and Remote Sensing (DRSRS), which span four decades of systematic reconnaissance flights across rangelands (Lamprey & Reid, 2004; Ogutu et al., 2009; Sitters et al., 2009; Bhola et al., 2012; Veldhuis et al., 2019).

Like population surveys, transect surveys are useful for observing patterns across seasons or years at broad spatial scales. Studies used transects to assess animal abundance, spatial distribution, habitat use, and sample forage conditions. Study areas were also large, ranging from 143 km^2 to 6,650 km^2. Studies varied in temporal scale: some collected data every month for decades, whereas others repeated data collection just twice over a single year (Ogutu et al., 2014; Green et al., 2019; Kiffner et al., 2020; Keesing et al., 2018). No transect data collection occurred at a frequency greater than biweekly.

Relatively few studies deployed telemetry (n = 6 studies) or camera trap methods (n = 2 studies) (Figure 2). When these methods appeared in our review, they captured data at higher temporal resolutions, often at the level of minutes or hours. For example, telemetry collars on hirola – a highly endangered antelope – provided hourly GPS fixes from individuals for 38 months, generating data on hirola resource selection that suggested an indirect relationship between cattle grazing, tree encroachment, and hirola decline (Ali et al., 2017). In a separate study, camera traps captured night-and-day images of water resources during periods of high and low pastoralist occupation, suggesting that pastoralists and wildlife coexist in overlapping space through temporal partitioning mechanisms (Connolly et al., 2021).

3.3. Inconsistent interpretations of evidence

There is a multiplicity of evidence across studies. Figure 3 shows that our process extracted 100 separate lines of evidence from the 46 studies. The Sankey diagram indicates that the largest proportion of evidence was interpreted negatively (n = 46 lines of evidence), followed by positively (n = 32) and neutrally (n = 22).

Two evidence types were dominant in our review: spatial relationships and abundance correlations (Fig. 2). This aligns with our observation in section 2.1, in which large-scale research methods – useful for capturing data on spatial patterns and abundance over time – were the most common.

Our review supports the observations of Butt and Turner (2012) where spatial overlap between wildlife and livestock is interpreted inconsistently (Fig. 2, inset). Figure 2 shows that evidence of spatial overlap was almost equally likely to be interpreted negatively, positively, or neutrally.

Spatial overlap was interpreted negatively (n = 6 lines of evidence) as a prerequisite for competition between wild herbivores and livestock. For example, Atickem and Loe (2014) found relatively high spatial and dietary overlap between mountain nyala and cattle, suggesting that competition with livestock caused observed declines in nyala abundance. Voeten and Prins (1999) identified spatial overlap between wildebeest, cattle, and zebra, and interpreted this as the basis for future competition: "...there is a strong potential for competition between the native wild species and cattle which consequently will have a negative effect on their coexistence" (Voeten and Prins 1999, 293).

Spatial overlap was also interpreted neutrally (n = 6 lines of evidence). This interpretation was most common when an author wrote that spatial overlap alone was insufficient to determine a negative relationship. Finally, the spatial overlap was almost as likely to be interpreted *positively* (n = 5 lines of evidence) (see inset, Figure 3). An example comes from Kenya, where high densities of some wild species overlapped with livestock on rangelands, appeared to benefit from reduced predation risk, and did not decline in abundance (Schuette et al., 2016).

These divergences may contribute to the debates over rangeland management, especially as PAs are often established on the assumption that wildlife and livestock should be spatially separated (see Discussion).

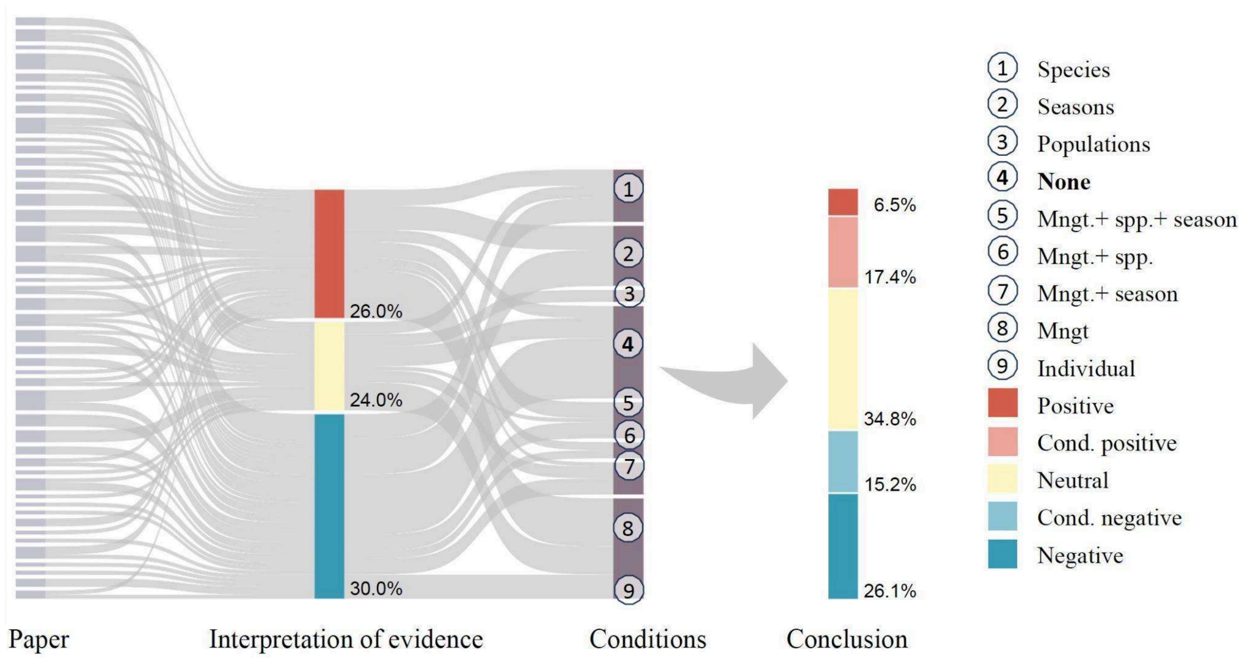

Figure 3. *Relationship between the paper's evidence; authors' interpretations of the evidence; the presence of mitigating conditional factors or qualifiers in the evidence; and the paper's conclusion on the wildlife-livestock relationship.*

Evidence is also commonly mediated by conditional factors. Out of the 100 lines of evidence we extracted, 77 were associated with at least one condition, and 24 of those were associated with more than one condition. This emphasizes the need for careful consideration of contextual and conditional factors when planning rangeland policy interventions.

Figure 3 shows the conditions present across our synthesis of evidence:

- **Management conditions:** Management conditions were associated with 49 lines of evidence from 22 studies, more than any other type of condition (Figure 3). Interestingly, positive evidence was *always* associated with a management condition; see Section 3.5.
- **Seasonal variations:** Evidence whose interpretation—either positive or negative—was conditional on the season was common (n = 32 lines of evidence from 12 studies, Figure 3). For example, multiple studies produced evidence that indicated a competitive relationship under dry conditions, but facilitation in wet conditions (Odadi et al., 2007; Mworia et al., 2008; Bhola et al., 2012; Odadi et al., 2011a).
- **Species variations:** We noted when evidence of the same type, in the same study, differed along species lines (n = 26 lines of evidence from 13 studies, Figure 3). For example, in a study examining livestock's impact on wildlife demography, positive demographic evidence was found for kongoni (*Alcelaphus busephalus*), while negative demographic evidence was observed for topi (*Damaliscus korrigum*) (Ogutu et al., 2011).
- **Population variations:** Only two studies within our review presented evidence that varied among subgroups or classes within a single population (Figure 3). An example includes evidence of spatial patterns among Grevy's zebra (*Equus grevyi*), revealing that territorial males and non-lactating females are unlikely to overlap with livestock, whereas bachelors and lactating females are more likely to do so (Low et al., 2009).

We found that land use and livestock management conditions influence positive relationships. Every positive line of evidence (n = 32) was associated with a management condition. This suggests that management conditions are important contributors to positive wildlife-livestock relationships and that understanding effective management strategies plays a crucial role in wildlife-livestock coexistence in East Africa.

Positive evidence in our review was associated with the following management conditions:

- **Stocking density:** Stocking density refers to the number of livestock present in an area; high densities of livestock are associated with forage depletion and degradation (e.g., Odadi et al., 2017). In our review, lower stocking densities were associated with positive evidence. For example, an enclosure experiment found that lowering the cattle density benefited zebra habitat use and improved cattle fitness (e.g., Wells et al., 2022).
- **Rotational or planned grazing:** Planned grazing includes methods such as rotating livestock through rangelands that have been divided, with or without physical fencing, into different grazing areas to promote forage recovery (e.g., Odadi et al., 2017). Rotational grazing was associated with positive evidence including improved species richness, forage conditions, and cattle fitness (e.g., Odadi et al., 2017). This was despite

comparatively higher livestock density in rotational grazing areas, suggesting that rotational grazing can mediate the negative impact of high stocking densities.

- **Land use and livestock management practices:** Authors investigated a broad range of land management practices, often comparing wildlife responses on a continuum from settled and cultivated land, to pastoral grazing lands, and finally wildlife-only conservation lands. Pastoral land management techniques were associated with a range of positive evidence types compared to settled and conservation lands, including reduced predation risk, reduced parasite loads, and higher forage quality (e.g., Georgiadis et al., 2007b; Keesing et al., 2018; Kiffner et al., 2020). However, wildlife living on pastoral lands was seen to make trade-offs, such as temporally partitioning resources to avoid humans and livestock (e.g., Schuette et al., 2016; Kiffner et al., 2020).

3.4. Most conclusions are neutral

We found the largest proportion of studies (n = 16) produced neutral conclusions on the wildlife-livestock relationship (Figure 3). Studies were categorized as neutral when they presented a balance of positive and negative evidence and discussed these in equal detail. This balance of evidence could be due to 1) changing seasonal conditions, 2) different responses between species, 3) different management conditions, or 4) all three (Figure 3).

Studies were also categorized as neutral if authors presented evidence neutrally and refrained from drawing overtly positive or negative conclusions. For example, when observing spatial overlap between Grevy's zebra (*Equus grevyi*) and livestock, Low et al. (2009) asserted that "an open question" remained as to whether this overlap suggested zebra-livestock competition. Similarly, Sundaresan et al. (2008) observed spatial non-overlap between Grevy's zebra and livestock but refrained from concluding that this harmed either zebra or livestock. In both instances, the authors deliberately chose neutral language that avoided "taking sides" in debates on the wildlife-livestock relationship or rangeland management.

Figure 3 reveals a large gap in the proportion of positive *evidence* and positive *conclusions*. While positive evidence comprises 26% of all lines of evidence, only 6.5% of study conclusions are categorically positive. This gap is smaller for negative evidence, which represents 30% of all lines of evidence and 26.1% of all conclusions.

This gap is partly explained by the absorption of positive lines of evidence into neutral conclusions (34.8% of conclusions, Figure 3). This happened when both positive and negative evidence were equally present in a single study and balanced into a neutral conclusion, as previously discussed. Additionally, there were more conditional positive conclusions than conditional negative conclusions (Figure 3). This implies that positive evidence tends to be presented with a degree of caution, often accompanied by discussions of conditional factors, whereas negative evidence is comparatively less discussed in terms of conditions.

3.5. Gaps in Current Understanding

Theories of wildlife-livestock incompatibility have contributed to a long-term perception of rangelands as degraded by livestock (Niamir-Fuller et al., 2012). The establishment of flagship PAs in Kenya, Tanzania, and Uganda followed this logic, evicting or denying grazing rights to pastoralists in the mid-twentieth century (Shetler, 2007; Infield et al., 2008; Butt, 2014; Moehlman et al., 2020). Evictions of people and livestock in the name of wildlife conservation persist today in East Africa (Amnesty International, 2023).

Researchers and pastoralists are increasingly challenging and resisting these perceptions and policies, but to date, there has been no review of the evidence from East Africa (Infield et al. 2008; Niamir-Fuller et al. 2012; Butt, 2014). Our systematic review analyzed and synthesized the evidence from four decades of empirical studies on the wildlife-livestock relationship in East African rangelands. We found three types of knowledge gaps: geographic, livestock species, and methodology.

Most studies are from Kenya, particularly the country's north-central regions, which are drier than the rest of Kenya. A wider geographic scope will address the heterogeneity of ecosystems and livestock-keeping cultures across East Africa, and perhaps more crucially, allow us to identify patterns in how social, economic, and political contexts influence the wildlife-livestock relationship.

Each country represented in our review (Kenya, Tanzania, Ethiopia, Zimbabwe, and Uganda) possesses a unique political and economic history that greatly influences the environmental conditions relevant to our research questions. For example, Homewood et al.'s (2001) comparative analysis of the Serengeti-Mara ecosystem, straddling Kenya and Tanzania, shows that land tenure policies and agricultural market incentives appear to drive wildebeest decline *only* in Kenya. Expanding opportunities for research in other countries and regions is essential for understanding how political and economic decisions change ecosystems and, in turn, influence both wildlife and livestock.

Our review also reveals a gap in understanding the relationships between wildlife and non-bovid livestock, particularly sheep and goats. A growing body of research indicates that East African pastoralists are shifting the composition of their herds to include more sheep and goats (O'Connor et al., 2015; Jandreau & Berkes, 2016; Green et al., 2019; Løvschal et al., 2019). Further, evidence in our review found that wildlife is more likely to co-occur on properties with cattle than on properties with sheep or goats, signaling an urgent need to investigate this relationship as sheep and goat populations increase (Keesing et al., 2018). Yet no studies in our review focused solely on the relationship between wild ungulates and non-bovid livestock (Table 4).

Rangelands are influenced by multi-scale ecological interactions (Western et al., 2020), but our review reveals a bias toward coarse-scale methods. We recommend an increased focus on empirical methods that generate evidence at finer spatial and temporal scales to complement the wealth of population surveys and transect data generated over decades. These methods provide snapshots of relevant variables at specific points in time. However, they do not fully capture scalar variability in the spatial and temporal distribution of resource selection that characterizes East African rangelands. Fine-scale information is also crucial for understanding niche habitat preferences and mechanisms that reduce competition by partitioning resources at different times of day (Frey et al., 2017; Schoener, 1974).

Methods and techniques to capture fine-scale animal relationships, including camera traps and telemetry, have become increasingly valuable in studying habitat niches and temporal behaviors in community ecology (Frey et al., 2017). Grazing preferences and forage behavior may vary widely at small scales, even when wildlife and livestock share the same habitat and feeding guild (Butt & Turner, 2012).

Temporal resource partitioning strategies are vital for coexistence between species, especially in the face of environmental stressors such as climate change, landscape transformation, and alterations to community composition (Schuette et al., 2016; Tyrrell et al., 2017; Frey et al., 2017; Connolly et al., 2021). Although temporal partitioning was not previously understood as a significant way to avoid competition, "partitioning time of activity may be one of the most relevant strategies for the coexistence of species" (Frey et al., 2017, 126). A lack of research on these fine-scale mechanisms contributes to uncertainty on these aspects of the relationship and obscures potential strategies for managing coexistence in these rangelands.

3.6. Contribution to Ongoing Debates

Widening the geographic and methodological scope of evidence from East Africa may add more appropriate contexts and nuance to debates about rangeland management. However, our review also revealed some differences in evidence interpretation and study conclusions, which may result from deeper logical and ideological inconsistencies.

<u>(i) Evidence discrepancies:</u> Our review provides a diversity of evidence on the wildlife-livestock relationship. The largest group of evidence was interpreted negatively, yet we observed

inconsistencies in the interpretation of some evidence types, notably spatial overlap (Figure 3). Different interpretations of similar evidence may derive from three sources of inconsistency: 1) methodological, 2) logical, and 3) ideological.

The observed bias toward coarse-scale methods poses a risk that causal relationships between wildlife and livestock may be inappropriately inferred, possibly favoring negative interpretations of evidence. For example, despite research that correlates a decline in wildlife with an increase in livestock over decades, some authors have concluded that land use changes, drought, and poaching are more likely to be responsible for the observed declines (Ottichilo et al., 2000a; Ottichilo et al., 2000b; Schieltz & Rubenstein, 2016). Coarse-scale methodologies are challenged in isolating these variables, further emphasizing the need for a multi-scale approach.

Inconsistent interpretations can also result from inconsistent *logic*, stemming from a lack of a rigorous, shared understanding of concepts. Butt and Turner (2012) describe conceptual vagueness across multiple studies of ecological competition, which can result in contradictory interpretations of spatial overlap. Spatial distribution models themselves can suffer from conceptual vagueness: in their review of terminology relating to species distribution modeling, Peterson and Soberón (2012) critiqued conceptual inconsistencies across these tools, finding that half of the studies in their review used incorrect terminology and contributed "many confusions and inappropriate conclusions" across the discipline (Peterson & Soberón, 2012).

Finally, differences in evidence interpretation may be the result of ideologies that continue to shape ecological research conducted across East Africa. For example, eight studies in our review collected data at the Mpala Research Centre in Laikipia, Kenya. In their analysis of Mpala, Griffiths et al. (2023) emphasize its ties to colonial-era practices of racial exclusion and perceptions of East African rangelands as "unspoiled wilderness," ignoring the historical presence of livestock and/or humanity. Such practices and perceptions partially justified the segregation of livestock from wildlife in the first place (Garland, 2008; Mbaria and Ogada, 2016; Griffiths et al., 2023). In these contexts, researchers may be unconsciously influenced by entrenched and unexamined ideologies and theories.

<u>(ii) Neutral conclusions and conditional factors emphasize nuance and context:</u> The largest proportion of conclusions in our review were neutral. We expected mostly negative conclusions due to the widely-held perception that livestock harms wildlife (Box 1). The enduring strength of that perception was referenced by many authors in our review (Young et al., 2005; Sitters et al., 2009; Charles et al., 2017; Nyamukuru, 2019; Connolly et al., 2021).

The prevalence of neutral conclusions in our review is important for several reasons. First, it indicates that a balance of positive and negative evidence was common within individual studies. This balance was often due to the presence of conditional factors: species-specific responses, changes in climate, and diverse management strategies that could produce contrary evidence even within the confines of a single study.

Second, neutral conclusions also reflect the nuanced nature of wildlife-livestock relationships in East Africa, emphasizing that ecological dynamics are not easily categorized as strictly positive or strictly negative (Young et al., 2018). Recognizing this complexity is essential to avoid oversimplification of ecological processes and to foster a more accurate representation of the many types of relationships between wildlife and livestock. However, it also reduces the generalizability of specific results and evidence (Young et al., 2018).

Third, neutral conclusions may be a conscious challenge on the part of authors to the enduring belief that wildlife and livestock are fundamentally incompatible, particularly as awareness grows regarding some of the social and ecological harms associated with strict wildlife-livestock separation in East Africa (Dowie, 2011; Butt, 2014; Moehlman, 2020). This underscores the influence of researcher attitudes, shifting ideologies, and social contexts on empirical conclusions about the wildlife-livestock relationship.

Neutral conclusions and abundant conditional factors suggest that any productive future debates must allow for a nuanced, conditional, and contextual understanding of the wildlife-livestock relationship. Acknowledging this nuance also suggests that there is no "silver bullet" approach for sustainable rangeland management (see di Virgilio et al., 2019), and our review emphasizes the need for context-specific research, even when it may not be generalizable across large geographies and heterogeneous environments.

4. Conclusion

East Africa's ecosystems, world-famous biodiversity, and controversial rangeland management policies make the region an important focal point for understanding the wildlife-livestock relationship. This systematic review is the first to analyze evidence on this relationship in this region and offers a comprehensive synthesis, analysis, and visual representation of the evidence.

Our review brings to light several lessons. First, we find gaps and opportunities for future research on the livestock-wildlife relationship in East Africa, including attention to non-bovid livestock, a greater emphasis on fine-scale methodologies, and an expansion of research in countries beyond Kenya (see Løvschal et al., 2019).

We also find that evidence based on spatial overlap is prone to inconsistent interpretation. Our review also echoes prior calls for all empirical research on this relationship to define key concepts, such as competition, to ensure consistent interpretation of evidence across studies (see Butt & Turner, 2012).

Contrary to the strong perception that livestock and wildlife fundamentally compete for resources, our review found a multiplicity of negative, positive, and neutral evidence on the wildlife-livestock relationship in East Africa (for a global review, see Schieltz & Rubenstein, 2016). The largest proportion of studies in our review were neutral in their overall conclusions, challenging a perception of inevitable antagonism between all wildlife and all livestock.

The presence of conditional factors across the evidence emphasizes that East African wildlife-livestock relationships are context-dependent and highly sensitive to seasonal variation and management techniques (see Riginos et al., 2012; Young et al., 2018). We also find an association of positive evidence with specific land use and livestock management conditions. This underlines the promise of management techniques in promoting wildlife-livestock coexistence. As debates persist on how to manage rangelands shared by wildlife, livestock, and people, this suggests that solutions-oriented policymakers, pastoralist peoples, and researchers should concentrate on identifying land and livestock management strategies that produce the best outcomes in their specific cultural and ecological contexts (see Holecheck et al., 2006; di Virgilio et al., 2019; Western et al., 2020; Pozo et al., 2021).

Our review should disturb the logic of rigid policies of wildlife-livestock separation, especially when these policies result in hostility, violence, or rights violations (Amnesty International, 2023). Future research and policy debates should embrace complexity and contextuality, rejecting oversimplifications and advocating for tailored research approaches suited to diverse environments and socio-ecological contexts.

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Appendix I

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Appendix II

paper_id	method	measurements	evidence_metrics	evidence_interpretation	conditions	paper_interpretation	paper_conclusion
bamford2014	transects	Spoor counts, dung counts	abundance_correlation	negative	management	conditional_negative	conditional_negative
moehlman2020	survey	Aerial census	abundance_correlation	positive	management+species	conditional_positive	conditional_positive
moehlman2020	survey	Aerial census	abundance_correlation	negative	management+species	conditional_positive	
moehlman2020	survey	Vegetation survey	forage_conditions	neutral	management+species	conditional_positive	
nyamukuru2019	experimental_plots	Dung counts	abundance_correlation	positive	species	positive	positive
nyamukuru2019	experimental_plots	Dung counts	abundance_correlation	negative	species	positive	
dublin2015	survey	Aerial census, rainfall records	abundance_correlation	negative	none	negative	negative
keesing2018	transects	Vegetation survey, dung counts, tick counts	abundance_correlation	positive	management	conditional_positive	conditional_positive
keesing2018	transects	Vegetation survey, dung counts, tick counts	abundance_correlation	negative	management	conditional_positive	
keesing2018	transects	Vegetation survey, dung counts, tick counts	forage_conditions	positive	management	conditional_positive	
keesing2018	transects	Vegetation survey, dung counts, tick counts	forage_conditions	negative	management	conditional_positive	
keesing2018	transects	Vegetation survey, dung counts, tick counts	disease_dynamics	positive	management	conditional_positive	
odadi2009	experimental_plots	Cattle bite rate, step rate in mixed plots	animal_behavior	negative	seasonal	neutral	neutral
odadi2009	experimental_plots	Cattle bite rate, step rate in mixed plots	animal_behavior	positive	seasonal	neutral	
odadi2009	experimental_plots	Cattle bite rate, step rate in mixed plots	forage_conditions	negative	seasonal	neutral	

odadi2009	experimental_ plots	Cattle bite rate, step rate in mixed plots	forage_conditio ns	positive	seasonal	neutral	
ogutu2014	survey	Ground census	spatial_non_ove rlap	negative	species	conditional_ne gative	conditi onal_n egativ e
ogutu2014	survey	Ground census	spatial_overlap	positive	species	conditional_ne gative	
bhola2012	survey	Aerial census, NDVI	spatial_non_ove rlap	negative	seasonal	neutral	neutral
bhola2012	survey	Aerial census, NDVI	spatial_overlap	positive	seasonal	neutral	
bhola2012	survey	Aerial census, NDVI	predation_risk	positive	seasonal	neutral	
odadi2017	transects	Dung counts, NDVI, herbaceous cover, plant basal gap, cattle weight gain	forage_conditio ns	positive	management	conditional_po sitive	conditi onal_p ositive
odadi2017	transects	Dung counts, NDVI, herbaceous cover, plant basal gap, cattle weight gain	demography_an d_fitness	positive	management	conditional_po sitive	
odadi2017	transects	Dung counts, NDVI, herbaceous cover, plant basal gap, cattle weight gain	richness_correla tion	positive	management	conditional_po sitive	
charles201 7	experimental_ plots	Dung counts, plant productivity cage measurements, NDVI, cattle weight gain	forage_conditio ns	positive	management	conditional_po sitive	conditi onal_po sitive
wells2022	experimental_ plots	Dung counts, bite characteristics, step rates	habitat_use	negative	management+ species+seaso nal	neutral	neutral
wells2022	experimental_ plots	Dung counts, bite characteristics, step rates	animal_behavio r	negative	management+ species+seaso nal	neutral	
wells2022	experimental_ plots	Dung counts, bite characteristics, step rates	animal_behavio r	positive	management+ species+seaso nal	neutral	
odadi2011 a	experimental_ plots	Weight gain, diet quality, herbaceous cover	demography_an d_fitness	negative	seasonal	neutral	neutral
odadi2011 a	experimental_ plots	Weight gain, diet quality, herbaceous cover	forage_conditio ns	negative	seasonal	neutral	

odadi2011a	experimental_plots	Weight gain, diet quality, herbaceous cover	demography_and_fitness	positive	seasonal	neutral	
odadi2011a	experimental_plots	Weight gain, diet quality, herbaceous cover	forage_conditions	positive	seasonal	neutral	
sundaresan2008	survey	Ground census, individual animal observation, grass color, grass height, bush density, location of bomas	spatial_non_overlap	neutral	population	neutral	neutral
odadi2011b	experimental_plots	Weight gain, bite rates, diet quality, herbaceous cover, gastrointestinal worm burden	demography_and_fitness	positive	none	positive	
odadi2011b	experimental_plots	Weight gain, bite rates, diet quality, herbaceous cover, gastrointestinal worm burden	animal_behavior	positive	management	positive	positive
odadi2011b	experimental_plots	Weight gain, bite rates, diet quality, herbaceous cover, gastrointestinal worm burden	disease_dynamics	positive	none	positive	
ogutu2011	transects	Ground census of herbivores, birth rate and recruitment rate observation, individual animal observation, aerial counts of livestock, aerial counts of bomas, aerial counts of huts	demography_and_fitness	positive	species	neutral	neutral
ogutu2011	transects	Ground census of herbivores, birth rate and recruitment rate observation, individual animal observation, aerial counts of livestock, aerial counts of bomas, aerial counts of huts	demography_and_fitness	negative	species	neutral	

gandiwa2013	survey	Aerial census of wildlife and livestock	abundance_correlation	neutral	species	negative	negative
gandiwa2013	survey	Aerial census of wildlife and livestock	spatial_overlap	negative	none	negative	
gandiwa2013	survey	Aerial census of wildlife and livestock	spatial_non_overlap	negative	none	negative	
schuette2016	transects	Ground census of herbivores, predators and wildlife across 4 land-use types	spatial_overlap	positive	management+species+seasonal	conditional_positive	conditional_positive
schuette2016	transects	Ground census of herbivores, predators and wildlife across 4 land-use types	spatial_non_overlap	negative	management+species+seasonal	conditional_positive	
schuette2016	transects	Ground census of herbivores, predators and wildlife across 4 land-use types	abundance_correlation	positive	management+species+seasonal	conditional_positive	
schuette2016	transects	Ground census of herbivores, predators and wildlife across 4 land-use types	predation_risk	neutral	management+species+seasonal	conditional_positive	
ogutu2010	survey	Ground census, aerial observation to map water, presence and location of bomas and water sources	spatial_non_overlap	neutral	management+species+seasonal	conditional_negative	conditional_negative
ogutu2010	survey	Ground census, aerial observation to map water, presence and location of bomas and water sources	spatial_overlap	negative	management+species+seasonal	conditional_negative	
georgiadis2007a	survey	Aerial census	abundance_correlation	neutral	management	neutral	neutral
tyrrell2017	transects	Ground census	spatial_overlap	neutral	management+seasonal	positive	positive
tyrrell2017	transects	Ground census	abundance_correlation	positive	management+seasonal	positive	

sitters2009	survey	Aerial census of wildlife and livestock, presence and location of water	spatial_overlap	neutral	none	neutral	neutral
sitters2009	survey	Aerial census of wildlife and livestock, presence and location of water	spatial_non_overlap	neutral	none	neutral	
kiffner2014	transects	Ground census	richness_correlation	positive	management	conditional_positive	conditional_positive
kiffner2014	transects	Ground census	richness_correlation	neutral	management	conditional_positive	
young2005	experimental_plots	Dung counts, presence or absence of herbaceous species	abundance_correlation	neutral	management	neutral	neutral
young2005	experimental_plots	Dung counts, presence or absence of herbaceous species	forage_conditions	neutral	management	neutral	
lamprey2004	survey	Aerial census, ground census, vegetation change	abundance_correlation	negative	management	conditional_negative	conditional_negative
lamprey2004	survey	Aerial census, ground census, vegetation change	predictive	negative	management	conditional_negative	
dunham2003	survey	Aerial census, ground census, individual animal observation, diet quality	abundance_correlation	negative	management	conditional_negative	conditional_negative
green2019	transects	Ground census, counts of bomas	abundance_correlation	negative	none	negative	negative
green2019	transects	Ground census, counts of bomas	richness_correlation	negative	none	negative	
ogutu2009	survey	Aerial census, counts of bomas and huts	abundance_correlation	negative	species	negative	negative
ogutu2009	survey	Aerial census, counts of bomas and huts	spatial_non_overlap	negative	management+species	negative	
bedelian2007	interviews	Interviews to determine Maasai pastoralists' perception of disease incidence and their	disease_dynamics	negative	seasonal	negative	negative

		livestock movements and avoidance of wildlife					
masiaine2021	camera_traps_continuous_recordings	Camera traps	habitat_use	negative	none	negative	negative
masiaine2021	camera_traps_continuous_recordings	Camera traps, counts of tourist camps, lodges and infrastructure, mapping of water sources	spatial_overlap	negative	species	negative	
masiaine2021	camera_traps_continuous_recordings	Camera traps, counts of tourist camps, lodges and infrastructure, mapping of water sources	spatial_non_overlap	neutral	species	negative	
odadi2007	experimental_plots	Bite ratios, vegetation sampling, percent canopy cover	animal_behavior	negative	seasonal	conditional_negative	conditional_negative
odadi2007	experimental_plots	Bite ratios, vegetation sampling, percent canopy cover	forage_conditions	negative	seasonal	conditional_negative	
prins1992	survey	Aerial census of observed stocking rate, possible stocking rate, human population growth rates	predictive	negative	none	negative	negative
atickem2014	transects	Dung counts	abundance_correlation	negative	none	negative	negative
atickem2014	telemetry	Foraging behavior, individual animal movements	spatial_overlap	negative	none	negative	
bonnington2007	transects	Ground census, spoor counts	abundance_correlation	negative	none	negative	negative
mworia2008	transects	Ground census, counts of farms and households	spatial_non_overlap	neutral	management+seasonal	neutral	neutral
mworia2008	transects	Ground census, counts of farms and households	forage_conditions	neutral	management	neutral	

mworia2008	transects	Ground census, counts of farms and households, herbaceous cover	abundance_correlation	neutral	management+seasonal	neutral	
veldhuis2019	experimental_plots	Grazing intensity, herbaceous cover	habitat_use	negative	management+seasonal	negative	negative
veldhuis2019	remote_sensing	NDVI, herbaceous cover	forage_conditions	negative	management+seasonal	negative	
veldhuis2019	survey	Aerial census	spatial_non_overlap	negative	management+seasonal	negative	
veldhuis2019	telemetry	Foraging behavior, individual animal movements	spatial_non_overlap	negative	management+seasonal	negative	
kanga2013	transects	Dung counts, vegetation sampling	spatial_overlap	negative	seasonal	negative	negative
kanga2013	transects	Dung counts, vegetation sampling	richness_correlation	negative	none	negative	
kanga2013	transects	Dung counts, vegetation sampling	forage_conditions	negative	none	negative	
low2009	survey	Ground census, individual animal movements	spatial_overlap	neutral	population	neutral	neutral
low2009	telemetry	Ground census, individual animal movements	spatial_overlap	neutral	population	neutral	
smith2022	telemetry	Individual animal movements	spatial_non_overlap	negative	none	negative	negative
smith2022	telemetry	Individual animal movements	spatial_overlap	neutral	none	negative	
voeten1999	survey	Foraging behavior, animal selection of vegetation characteristics	spatial_overlap	negative	seasonal	conditional_negative	conditional_negative
georgiadis2007b	survey	Aerial census, zebra demography	predation_risk	neutral	management+species	neutral	neutral
georgiadis2007b	survey	Aerial census, zebra demography	abundance_correlation	negative	management+species	neutral	
connolly2021	camera_traps_continuous_recordings	Livestock and wildlife usage of water sources	spatial_overlap	positive	management	conditional_positive	conditional_positive
connolly2021	camera_traps_continuous_recordings	Livestock and wildlife usage of water sources	animal_behavior	positive	management	conditional_positive	

<table>
<tr><td>ali2017</td><td>remote_sensing</td><td>Vegetation survey</td><td>forage_conditions</td><td>negative</td><td>none</td><td>neutral</td><td rowspan="2">neutral</td></tr>
<tr><td>ali2017</td><td>telemetry</td><td>Individual animal movements</td><td>spatial_overlap</td><td>positive</td><td>none</td><td>neutral</td></tr>
<tr><td>duporge2022</td><td>telemetry</td><td>Individual animal movements (through space and time)</td><td>animal_behavior</td><td>neutral</td><td>none</td><td>neutral</td><td>neutral</td></tr>
<tr><td>groom2013</td><td>transects</td><td>Ground census, herbaceous cover, grazing pressure (grass biomass)</td><td>abundance_correlation</td><td>neutral</td><td>none</td><td>neutral</td><td rowspan="3">neutral</td></tr>
<tr><td>groom2013</td><td>transects</td><td>Ground census, herbaceous cover, grazing pressure (grass biomass)</td><td>forage_conditions</td><td>neutral</td><td>management</td><td>neutral</td></tr>
<tr><td>groom2013</td><td>transects</td><td>Ground census, herbaceous cover, grazing pressure (grass biomass)</td><td>spatial_overlap</td><td>neutral</td><td>management</td><td>neutral</td></tr>
<tr><td>kiffner2020</td><td>transects</td><td>Ground census</td><td>abundance_correlation</td><td>positive</td><td>management+ species</td><td>conditional_positive</td><td>conditional_positive</td></tr>
<tr><td>oconnor2015</td><td>survey</td><td>Ground census, animal behavior observation</td><td>animal_behavior</td><td>positive</td><td>management</td><td>neutral</td><td>neutral</td></tr>
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