Apex Predators in the Anthropocene:
African Large Carnivore Ecology at the Human-Wildlife Interface

by

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Abstract

As anthropogenic pressures expand to permeate landscapes worldwide, sometimes with synergistic impacts, wildlife must navigate human-dominated landscapes and novel environmental regimes to survive. In this dissertation, I examine how complex human-caused environmental changes alter wildlife distributions, behaviors, and interactions, as well as the consequences of these changes for wildlife conflict with human communities. I focus on African large carnivores because of their ecological and conservation importance, using insights from ecological theory to contextualize large carnivore interactions with other wildlife, livestock, and people. Large carnivores are particularly at risk from human pressures due to long life histories, high energetic requirements, and the harm they can inflict on human livelihoods. Avoiding the risks posed by humans leads large carnivores to modify their ecological roles as top-down ecosystem regulators, potentially causing cascading impacts that restructure community processes. In Chapter II, I explore the spatiotemporal responses of three large carnivores and their prey to human use of a protected area in West Africa. Overall, wildlife avoided humans by changing the timing of their daily activity. By conducting a novel analysis on an extensive camera survey dataset, I found that human presence disrupted the overlap between predators and their prey, which could change prey selection and subsequent ecosystem processes. However, human presence is just one aspect of human-caused changes to wildlife habitats. In Chapter III, I synthesized the spatiotemporal responses of African lions (*Panthera leo*) to the multi-faceted effects of human disturbance across their range using a systematic meta-analysis of 23 studies across 30 sites. I found that lions consistently avoided the pressures of human-dominated landscapes in space and time, limiting

lions' spatiotemporal niche and likely reducing their ecological impacts as predators. However, the risks of human encounters appeared to be outweighed by lions' metabolic needs, resulting in increased overlap with human-dominated areas when primary resources were scarce. Additionally, lions avoided human disturbance more strongly at sites with high livestock production, signaling that livestock presence displaces wildlife or that lions are using behavioral strategies to target livestock as prey. To better understand the tangible impacts of how changing resource availabilities cascade to influence human-carnivore conflict, Chapter IV combines remotely sensed environmental measures with empirical data on prey availability and livestock depredation by lions in the Makgadikgadi Pans ecosystem in northern Botswana. I found that the incidence of livestock depredation by lions was highest at times of primary resource scarcity, including reduced primary production and water availability. Though changes in prey availability are commonly used to explain links between primary resources and livestock depredation, we did not find a direct link between wild prey availability and livestock depredation rates despite prey availability being strongly driven by primary productivity in the study area. The results of Chapter IV suggest that livestock depredation may be more strongly influenced by livestock and lion responses to resource availabilities, a process that was highlighted as a likely contributor to conflict in Chapter III but is overlooked in most human-carnivore conflict studies. By examining bottom-up drivers of conflict at fine temporal scales, Chapter IV expands our understanding of the fundamental role of global change in driving human-lion conflict across Africa. Overall, my dissertation thoroughly examines the consequences of human pressures on the ecological roles of lions and other large carnivores, highlighting how humans directly and indirectly modify their behaviors and interspecific interactions.

Chapter I

Introduction

Wildlife around the world are facing multi-faceted threats driven by human-caused environmental changes that define the Anthropocene (Brook *et al.* 2008), culminating in extinction rates for modern vertebrates up to 100 times higher than background estimates (Ceballos *et al.* 2015; De Vos *et al.* 2015; Ellis 2019). Where wildlife persist, their habitats are becoming increasingly disturbed by human activities and environmental changes (Pecl *et al.* 2017; Jones *et al.* 2018). While wildlife can respond to these pressures by modifying their behaviors along multiple axes – including altering movement patterns (Tucker *et al.* 2018) and activity timing (Gaynor *et al.* 2018; Gilbert *et al.* 2023) – these changes are not always adaptive and can restructure wildlife communities as well as their ecological interactions and impacts on ecosystems (Carthey & Blumstein 2018; Guiden *et al.* 2019; Sebastián-González *et al.* 2019; Santini & Isaac 2021; Merkle *et al.* 2022; Moore *et al.* 2022). In this dissertation, I examine how complex human-caused environmental changes alter wildlife distributions, behaviors, and interactions – as well as the consequences of these changes for wildlife conflict with humans – with a focus on large carnivores in Africa because of their ecological and conservation importance.

Large terrestrial carnivores are widespread and play a fundamental role in structuring ecosystems via top-down processes of predation and indirect fear effects (Ripple *et al.* 2014). Yet, large carnivores are of particular conservation concern because of their expansive home ranges that often overlap with human activities, high metabolic needs that generate conflict with people over shared resources (such as ungulate herbivores), and slow life histories that leave them especially vulnerable to population perturbations (Cardillo *et al.* 2004, 2005; Dirzo *et al.* 2014; Wolf & Ripple 2016). Given their ecological importance and heightened risks of extirpation, there is a dire need to examine the cascading impacts of human disturbances and ongoing climate changes on the ecology of large carnivores, including their ability – or lack thereof – to adapt to human pressures and resultant changes in interspecific interactions that structure ecosystems.

Toward this goal, my work first takes a community-level approach to assessing the impacts of human presence on predator-prey interactions. In **Chapter II**, I explored the spatiotemporal responses of three African large carnivores and their prey to human use of a protected area. By conducting a novel analysis on an extensive camera survey dataset, I found that humans disrupt the overlap between predators and their prey by causing shifts in wildlife temporal activity, potentially leading to changes in prey selection and subsequent ecosystem processes. While Chapter II is a case study demonstrating one essential mechanism through which large carnivores can adaptively respond to human disturbance (i.e., temporal avoidance of human encounters), it does not fully capture the wide range of human disturbances that impact ecosystems and subsequent heterogeneity in wildlife responses.

In addition to direct human presence, human-caused environmental changes such as habitat destruction and conversion, climatic regime shifts, and ecosystem management interventions can lead to modified wildlife activity (Brook *et al.* 2008; Tucker *et al.* 2018). In **Chapter III**, I synthesized the multi-faceted effects of human disturbance on the spatiotemporal activity of African lions (*Panthera leo*) across their contemporary range. Using a systematic meta-analysis of 23 studies at 31 sites, I assessed the extent to which the responses of lions to disturbance are influenced by tradeoffs between resource availability and anthropogenic risks. Although lions exhibited both spatial and temporal avoidance of human disturbance, these responses depended on the availability of resources at a given study site. Resource limitation appeared to outweigh the risks of human disturbance, leading to increased overlap between lions and people. By limiting the spatiotemporal niches of large carnivores, the ongoing global expansion of human impacts threatens to downgrade their ecological function across a range of environmental conditions. Given projections for climate change to intensify resource scarcity across space and time (Hulme *et al.* 2001; Dixon *et al.* 2003; Wu *et al.* 2021), the observed responses of lions also threaten to escalate human-lion conflict in many areas and intensify the risks of lion extinction.

Conflict between large carnivores and humans is one of the leading threats to carnivore conservation and places severe burdens on human livelihoods (Treves & Karanth 2003; Braczkowski *et al.* 2023). Despite advances in conflict mitigation techniques, coexistence between people and large carnivores remains a serious challenge at a global scale (Carter & Linnell 2016). Climate change has recently been identified as an underlying driver of intensifying human-wildlife conflict, primarily due to the ongoing redistribution and limitation of primary resources in space and time and the effects of these changes on wildlife distributions and behaviors (Abrahms *et al.* 2023). Building on the observed responses of lions to resource availability in Chapter III, **Chapter IV** used insights from ecological theory to explore how changes in resource availability over time affect levels of human-lion conflict in a case study from northern Botswana. Likely due to the complex responses of lions, wild prey, and livestock to resource scarcity, I found that livestock depredation by lions was intensified by reductions in forage and water resources. Human-wildlife conflict is ultimately the outcome of complex ecological interactions in coupled social-ecological systems, and the results of this dissertation highlight the need to incorporate both humans and their impacts into ecological theory to safeguard human livelihoods, protect threatened species, and ultimately achieve human-wildlife coexistence (Bagchi 2018; Miller & Schmitz 2019; Wilkinson *et al.* 2020).

Taken together, this dissertation uses a variety of tools and approaches to explore the multifaceted impacts of human disturbances and environmental change on wildlife communities. This work demonstrates that humans can modify ecosystems in many complex ways, including by altering wildlife spatiotemporal activity and modifying primary resource availabilities that govern animal distributions. Achieving coexistence between wildlife and people in the face of ongoing global change requires integrating often synergistic human and wildlife behaviors into a cohesive social-ecological framework, and it is imperative that we harness insights and approaches from both ecological theory and social science to do so.

Chapter II

Humans Disrupt Access to Prey for Large African Carnivores

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Abstract

Wildlife respond to human presence by adjusting their temporal niche, possibly modifying encounter rates among species and trophic dynamics that structure communities. We assessed wildlife diel activity responses to human presence and consequential changes in predator-prey overlap using 10,325 detections of 3 large carnivores and 11 ungulates across 21,430 camera trap-nights in West Africa. Over two-thirds of species exhibited diel responses to mainly diurnal human presence, with ungulate nocturnal activity increasing by 7.1%. Rather than traditional pairwise predator-prey diel comparisons, we considered spatiotemporally explicit predator access to several prey resources to evaluate community-level trophic responses to human presence. Although leopard prey access was not affected by humans, lion and spotted hyena access to 3 prey species significantly increased when prey increased their nocturnal activity to avoid humans. Human presence considerably influenced the composition of available prey, with implications for prey selection, demonstrating how humans perturb ecological processes via behavioral modifications.

Introduction

The diel activity of wildlife can adaptively respond to their environment by partitioning time to maximize survival and limit exposure to risks, producing a species' temporal niche (Bennie *et al.* 2014; van der Vinne *et al.* 2019). Prey commonly employ predator avoidance strategies along the temporal niche axis (Kohl *et al.* 2019), which is contrasted by predators selecting for temporal activity patterns that maximize hunting success and minimize competitive encounters (Cozzi *et al.* 2012; Dröge *et al.* 2017). As a result, large carnivores are predominantly nocturnal while ungulates often exhibit more diurnal behaviour, though neither exclusively so. However, pervasive human pressures disrupt individual behaviours that facilitate coexistence of predator and prey populations alike (Wolf & Ripple 2016; Shamoon *et al.* 2018; Xiao *et al.* 2018; Sévêque *et al.* 2020). How human-induced responses of many species cascade to alter the dynamics of predation and other ecological interactions at the community level remains understudied (Guiden *et al.* 2019).

The fear of humans can suppress spatiotemporal activity in both carnivores and herbivores with cascading impacts to lower trophic levels (Dorresteijn *et al.* 2015; Gaynor *et al.* 2018; Suraci *et al.* 2019a). Specifically, human presence engenders shifts in diel activity patterns across guilds, altering their temporal niche to incorporate avoidance of human encounters (Gaynor *et al.* 2018; Frey *et al.* 2020). Human activities concentrated in the day and predator activity at night reduce the availability of temporal refugia for prey from risky encounters, thus constraining species' abilities to optimize activity along the temporal niche axis (Kohl *et al.* 2019; van der Vinne *et al.* 2019). As predator and prey species alter their diel activity to adaptively respond to human presence, predator-prey temporal overlap and resulting encounter rates are likely to be changed (Patten *et al.* 2019), thus altering predator access to a suite of prey resources (Fig. 2-1). Such perturbations to predator-prey dynamics can have cascading impacts that alter population regulation, habitat structure, and various ecosystem processes, such as carbon storage, herbivory and seed dispersal (Pringle *et al.* 2007; Terborgh *et al.* 2008; Asner *et al.* 2009; Schmitz *et al.* 2018; Atkins *et al.* 2019).

If wildlife modify their temporal niche to avoid pressures associated with human presence, predators and prey will exhibit increased nocturnal activity at both the species and guild levels (Gaynor et al., 2018). If all species respond to humans similarly, human avoidance further predicts: 1) intensified predator-prey overlap overall, and 2) a greater diversity of prey species available to predators as previously diurnal species adopt nocturnal behaviours. Increasing the diversity of accessible prey would likely result in diminished predation rates on individual species, given that prey selection by carnivores is influenced in part by prey species' availability relative to other sympatric prey and the diversity of the prey community (Sinclair *et al.* 2003; Owen-Smith & Mills 2008). However, avoidance of humans may not be ubiquitous across species given species have different vulnerabilities to humans (Tablado & Jenni 2017). Thus, the prevalence of human avoidance among species is likely to determine the nature of community-level predator-prey outcomes.

Here, we evaluated the effects of human presence on the diel activity of predators and prey and consequential difference in predator-prey relationships using a novel method to assess predator-prey overlap at a community scale. We executed a systematic camera survey spanning 13,100-km^2 of the W-Arly-Pendjari (WAP) complex in West Africa across 21,430 trap-nights, obtaining detections of both wildlife and humans. We used occupancy modelling to determine areas of low and high human use within the study area and evaluate spatially explicit responses in species' behaviour and potential alterations to trophic interactions. Specifically, we tested for differences in diel activity patterns and nocturnal behaviours for three large carnivores (African lions, spotted hyenas, and African leopards) and 11 ungulate species between areas of low and high human presence. We also evaluated the effects of human presence on the overall temporal overlap (Δ) between each predator and its prey, as well as assessed differences in the relative overlap between predators and each individual prey species. We determined: i) how carnivores and ungulates adjusted their temporal niche in response to human presence, and ii) how apex predator access to prey species was influenced by human presence.

Previous works often investigate temporal overlap of predators and prey in a pairwise manner (Linkie & Ridout 2011; Ramesh *et al.* 2012; Patten *et al.* 2019). However, such an approach does not consider the overall composition of resources available to predators and the relative contributions of individual prey species. Higher-order interactions beyond pairwise predator-prey relationships likely contribute to determining community structure and coexistence among species (Levine *et al.* 2017). We combatted these limitations by extending beyond pairwise comparisons to consider predator-prey interactions at the community level by aggregating temporal activity among ungulates, providing a more ecologically realistic depiction of overlap between predators and their prey. Specifically, we used bootstrapped kernel density distributions of predator and prey diel activity to calculate the overlap between each predator-prey pair relative to the overall available prey (percent area under the predator diel curve, PAUC), which was generated by aggregating prey activity curves and then scaling the prey activity (kernel density estimates) to each predator. PAUC represents a metric of relative prey access for the apex predator, as it provides insight into the times of day that encounters between the predator and prey species are most likely to occur based on the temporal activity of both. In this new approach to assess the spatially explicit temporal responses of predators and their prey to humans, we elucidate the community-level effects of humans on trophic interactions and their implications for ecosystem regulation by large carnivores.

Methods

Study area

We conducted our study in the W-Arly-Pendjari (WAP) protected area complex that spans 26,515-km^2 in the transboundary region of Burkina Faso, Niger, and Benin (0°E-3° E, 10°N-13°N; Fig. 2-1a). The complex contains 5 national parks (54% of total area), 14 hunting concessions (40%), and 1 faunal reserve (6%). Our study area within WAP comprised three national parks and 11 hunting concessions in Burkina Faso and Niger across ca. 13,100-km^2 (Fig. 2-2a). Trophy hunting of many ungulate species and African lions (*Panthera leo*) is permitted in hunting concessions, while all hunting is illegal in the national parks and reserves in the complex. Other human activities in the park include livestock herding, resource extraction, recreation, and poaching (Sogbohossou *et al.* 2011; Miller *et al.* 2015; Harris *et al.* 2019). Recently, Harris et al. (Harris *et al.* 2019) reported 4 large carnivore species (African lion, African leopard *Panthera pardus*, spotted hyena *Crocuta crocuta,* and cheetah *Acinonyx jubatus*) and 17 ungulate species belonging to the superorder Ungulata in the three national parks included in our study area from an extensive camera trap survey. Cheetahs were detected only once, while wild dogs (*Lycaon pictus*) were not reported in the survey area. WAP has an arid climate and consists predominantly of Sudanian and Sahel savannas, with savanna accounting for ca. 90% of the habitat cover in the study area (Lamarque 2004; Mills *et al.* 2020). We conducted our survey in the drier northern portion of WAP during the dry season with average monthly rainfall ranging from 0-1 mm in February to 42-91 mm in June (Fick & Hijmans 2017). Though our study design may limit inferences to dry season conditions, evidence suggests that large African herbivores show similar overall temporal activity distributions as seasons change (Owen-Smith *et al.* 2010).

Camera survey

We systematically deployed 238 white-flash and infrared motion-sensor cameras (Reconyx© [Holmen, WI] PC800, PC850, PC900) within 10x10-km grid cells across our study area to assess effects of human presence on diel activity within the wildlife community. A single unbaited camera was placed within 2-km of the centroid in a total of 204 sampled grid cells over 3 survey seasons from January-June in 2016-2018 (Appendix A, Fig. S2-1). Camera stations within cells that were surveyed in multiple years were not necessarily placed in the same location both years, but they were placed within the same 2-km buffer and are considered representative of the grid cell each year. Species identifications from camera images were validated by two members of the Applied Wildlife Ecology (AWE) Lab at the University of Michigan. We excluded false triggers, unidentifiable images, research team, and park staff from analyses. To ensure robustness in our analyses, we combined all remaining human images into a single 'Human' categorization representing a variety of human activities observed in WAP (e.g., livestock herding, resource

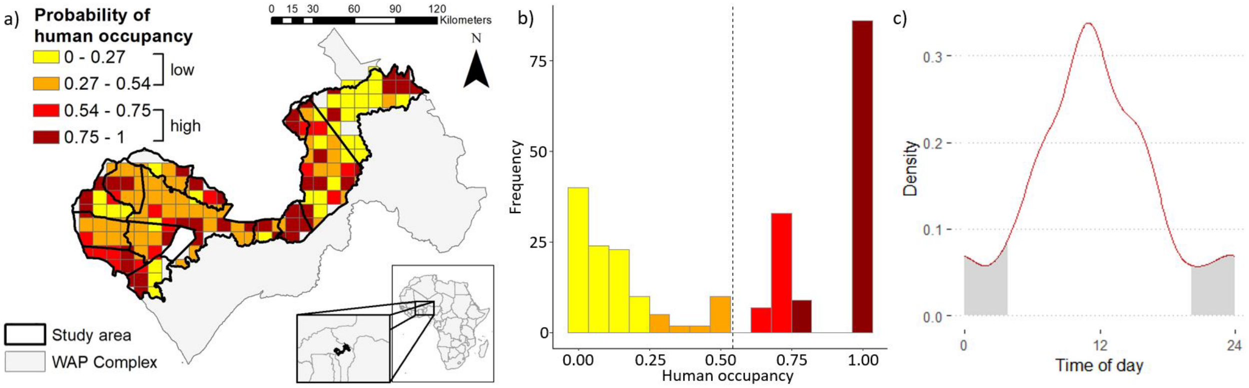

Figure 2-1: a) Map of study area within the W-Arly-Pendjari protected area complex in Burkina Faso and Niger, West Africa with surveyed 10-km^2 grid cells. Color depicts estimated levels of human occupancy within the study area, averaged across years for grid cells surveyed in multiple years. b) Corresponding frequencies of grid-level human occupancy for 3 survey years, with dotted line depicting mean human occupancy (0.54). c) Human diel activity kernel density distribution from camera detections.

gathering, recreation, poaching, and hunting). Our work is not human subjects research requiring IRB review, though we remain grateful to authorities granting permission for our research and their efforts to manage coupled human-natural ecosystems. (see Appendix A, Fig. S2-1; Mills et al. 2020 and Harris et al. 2019 for additional methods on camera deployment and image processing). Due to limited detections for some species, we aggregated survey data from all 3 years into a single data. We accounted for temporal variation in human space use during the subsequent modeling process, and previous work suggests little annual variation in wildlife activity (Mills *et al.* 2020). We created independence of species triggers using a 30-minute quiet period between detection events using the 'camtrapR' package in R 3.5.1 (http://www.r-project.org) (Niedballa *et al.* 2016), and we assumed detections to be a random sample of each species' underlying activity distribution (Linkie & Ridout 2011).

Human occupancy models

We constructed single-season, single-species occupancy models to designate WAP into areas of low and high human use. We chose to use single-season models to assess the overall distribution of human space use across the study area, as opposed to multi-season occupancy models which also estimate extinction/colonisation rates that is not necessary for our objective. Instead, we included year as covariate in single species models to assess temporal variation in human occupancy patterns. Occupancy models account for spatial heterogeneity in human presence across the study area, facilitating investigation into the behavioural responses of sympatric wildlife. We separated detection/non-detection data for humans into 2-week observation periods, which were modelled as independent surveys to account for imperfect detection. Our occupancy models first modelled the detection process (*p*) using covariates expected to influence detection while holding occupancy (Ψ) constant, and then modelled human occupancy by incorporating grouping variables among which Ψ may vary.

The global detection model included covariates related to survey design and the environment that we expected to influence the detection of humans: % savanna habitat (SAV), survey year (YR), trap-nights (TN), camera type (CAM), management type (MGMT), and site (i.e., one of 14 individual parks or concessions; SITE). MGMT was a binary variable that distinguished national parks from hunting concessions. Human occupancy was modelled with only grouping variables: MGMT, YR, and SITE. We included YR as a covariate to account for temporal variation in site use or detection, as cells surveyed in multiple years were considered separate sites for our single-season model. A grid cell surveyed in multiple years could, therefore, have different levels of occupancy between surveys. Variables included in the top-performing occupancy and detection model(s) are considered those which best described the spatial variation in human detection and site use. We evaluated the support for all combinations of detection and occupancy covariates using the Akaike information criterion corrected for small sample sizes (AICc). We selected the top-performing detection and occupancy models as those with ΔAICc < 2 compared to the lowest AICc model. We assessed goodness-of-fit of the top-performing models using 1,000 parametric bootstraps of a χ^2 test statistic appropriate for binary data and estimated the $\hat{c}$ statistic to ensure the data were not over-dispersed (Fiske & Chandler 2017). We created all detection and occupancy models using the ‘unmarked’ package and conducted model selection using the ‘MuMIn’ package in R (Fiske & Chandler 2011; Bartoń 2019).

We extracted cell-specific latent occupancy probabilities, representing probabilities of site use by humans because the 10-km^2 grid cells do not meet the assumption of closure, from the top-performing (lowest AICc) occupancy model corrected for imperfect detection (MacKenzie *et al.*

2016). From those estimates, we categorized grid cells as either low or high human use. We delineated the threshold for human use using the mean value of human occupancy. We chose to use the mean occupancy as the threshold value because of the bimodal distribution of occupancy values and to facilitate comparisons between similar sample sizes of low and high human use grid cells (Fig. 2-2b). We also conducted a sensitivity analysis to evaluate the selected threshold by repeating our analyses using thresholds ± 0.1, as described in the following section.

Temporal analyses

Using detection timestamps from our camera survey, we compared the temporal activity patterns for apex predators (lions, leopards, and hyenas) and sympatric ungulates between areas of low and high human use. We included 12 ungulate species: savanna buffalo (*Syncerus caffer brachyceros)*, roan antelope (*Hippotragus equinus koba)*, western hartebeest (*Alcelaphus buselaphus major*), waterbuck (*Kobus ellipsiprymnus defassa)*, Buffon's kob (*Kobus kob kob)*, Bohor reedbuck (*Redunca redunca)*, bushbuck (*Tragelaphus sylvaticus)*, aardvark (*Orycteropus afer)*, warthog (*Phacochoerus africanus)*, oribi (*Ourebia ourebi)*, red-flanked duiker (*Cephalophus rufilatus),* and common duiker (*Sylvicapra grimmia*). We excluded four ungulate species from analysis in our study: topi (*Damaliscus korrigum jimela*) and red-fronted gazelle (*Eudorcas rufifrons*) due to few detections (< 50), and elephant (*Loxodonta africana*) and hippopotamus (*Hippopotamus amphibius*) due to large body sizes that make them unlikely prey items for large carnivores. Duiker species were aggregated due to difficulty distinguishing the two in camera trap images, resulting in 11 total ungulate species in our analyses. Previous work in this system supports estimation of prey availability from camera trap data in that predator space use is heavily influenced by prey availability as estimated from camera trap detections (Mills *et al.* 2020).

Further, temporal activity overlap between species are directly influences the strength of interspecific interactions (Kronfeld-Schor *et al.* 2017).

We used kernel density estimation to produce diel activity curves representing a species' realized temporal niche in both human use zones for each of the 16 species. We first tested for differences in these activity distributions between low and high human use areas for all individual species and for each guild (representing the overall available prey base and predation pressures) by calculating the probability that two sets of circular observations come from the same distribution with a bootstrapped randomization test (Ridout & Linkie 2009). Significant differences in temporal activities were evaluated as p-value < 0.05. We conducted a sensitivity analysis by adjusting the human occupancy threshold ± 0.1 and repeating this test for all species and both guilds to ensure robustness of our results (Appendix A, Table S2-3).

Using 10,000 parametric bootstraps of the temporal distribution models, we then calculated the area under the diel activity curves to determine the proportion of each species' activity that occurred during nocturnal hours (two hours after sunset to two hours before sunrise). We used the sunrise (05:41) and sunset (18:06) times from the median date of our surveys (April 4, 2018) at the survey area centroid to define nocturnal hours. To test if wildlife nocturnality differed in response to human presence, we compared the bootstrapped 95% confidence intervals (CIs) of the difference in nocturnality for each species and overall guilds between low and high human areas where a significant difference was observed when the CI did not overlap 0.

We used the coefficient of overlap (Δ) to quantify the total temporal overlap between each apex predator and their associated prey from circular activity distributions. Buffalo was excluded from the prey list of African leopards due to large body size. All other prey species were aggregated to produce a single diel activity curve of all prey for comparison to predator activity. We chose the specific estimator based on the minimum sample size of detections for both guilds to contrast human use levels (Δ_1 if $N < 75$, Δ_4 if $N > 75$). Values of Δ range from 0-1 where 0 represents no temporal overlap and 1 represents complete overlap or identical temporal niche between predators and their prey. We used 10,000 bootstrapped estimates to extract the bias-corrected 95% CIs of Δ. We compared CIs of Δ between human use levels for each species to assess differences in predator-prey overlap in response to human occurrence. Non-overlapping CIs between human use levels indicated that the overall temporal overlap of predators with their prey was significantly altered by human presence. Temporal analyses were conducted using the ‘activity’ and ‘overlap’ packages in R (Ridout & Linkie 2009; Rowcliffe 2019).

Predator access to prey

After determining overlap between predators and their prey as well as shifts induced by humans, we determined the implications for predator access to prey. To our knowledge, we developed a new method to assess species-specific prey access for predators that is temporally explicit over the diel period, enabling assessment of differences in the composition and diversity of accessible prey for predators resulting from responses to humans in both guilds. We first combined (i.e., stacked) the bootstrapped temporal kernel density curves for individual prey to produce a total diel activity curve for prey, but this time maintaining each species’ contributions to overall prey activity. We then multiplied each prey species’ proportional contribution to prey activity at a given point in the diel cycle by the corresponding kernel density activity value of each respective apex predator. This method produced a discrete area under the predator temporal activity curve for each prey species of a given apex predator (percent area under curve, PAUC), where each prey species’ value represents the relative temporal overlap between the apex predator and that prey species throughout the day. We used these PAUC values to assess whether predator access to individual prey species, relative to all available prey, were different between low and high human areas by calculating the difference in prey access (ΔPAUC) for each predator/prey combination between areas of low and high human use. To determine if prey access was significantly differed between human presence levels, we compared bootstrapped estimates and 95% CIs of ΔPAUC. Finally, we used a Fligner-Killeen test for homogeneity of variance to determine how the diversity of each predator's accessible prey differed in association with human presence based on PAUC values. Lower variance in prey access represents more evenness (i.e., more diversity) in access across prey items, while higher variance indicates prey access is higher for a subset of species compared to others.

Results

Our camera survey yielded 786 and 10,325 detections of apex predators and ungulates, respectively, over 21,430 trap-nights throughout our West African study system (Appendix A, Table S2-1). Spotted hyenas are the dominant predator in the system with 6 times more detections than either African lions or leopards. Warthog, reedbuck, and bushbuck were the most commonly observed ungulates, each detected over 1,000 times.

We obtained 350 detections of humans in 69 out 204 surveyed 10-km^2 grid cells, leading to a naïve human occupancy of 0.34. Humans exhibited mostly diurnal activity with 80.3% of detections occurring between sunrise and sunset (Fig. 2-2c). Accounting for imperfect detection, model selection resulted in four competing top models ($\Delta AICc < 2$) for human occupancy (Appendix A, Table S2-2). Detection of humans primarily varied among years and sites and was higher in non-savanna habitat (top model goodness-of-fit p-value = 0.327). Human occupancy was pervasive, but heterogeneous within the study area (Fig. 2-2a; $\bar{\Psi} = 0.54$ SE 0.41), ranging from 0.0006 to 1 with highest frequencies near these extremes (Fig. 2-2b). Using the mean value of occupancy as a pressure threshold, we designated 108 of 204 grid cells as having high human use (occupancy > 0.54).

Human avoidance responses

Human presence generated marked modifications in the temporal niches of sympatric wildlife, with both guilds exhibiting human avoidance behaviours overall. Carnivores and ungulates showed significantly different diel activity patterns between low and high human use (carnivores *p*-value = 0.017; ungulates *p*-value < 0.001; Fig. 2-3). Over two-thirds (10 out of 14) of the mammal species in the study exhibited significant differences in their diel activity patterns in response to human presence (leopards, hyenas, and 8 ungulates; Fig. 2-3; Appendix A, Table S2-3). Ungulates overall were 7.1% (95% CI ± 1.7%) more active at night in high human areas, while carnivores showed a slight but non-significant increase in night-time activity of 3.9% (± 5.7%). Specifically, we observed significantly higher nocturnal activity with high human use for reedbuck

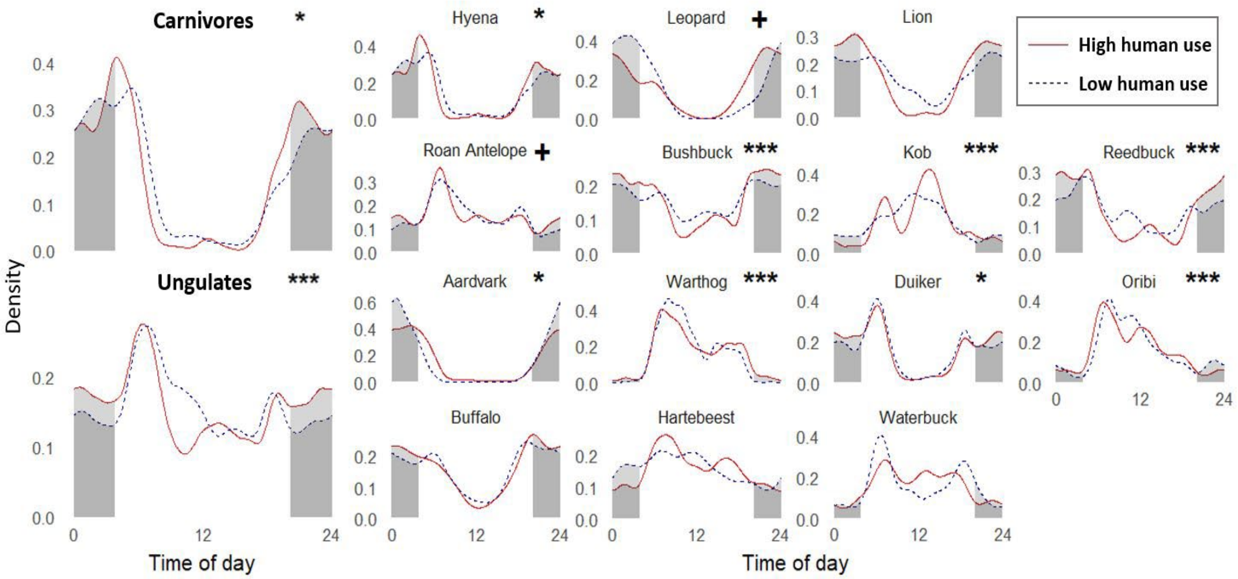

Figure 2-2: Temporal activity kernel density curves for large carnivores (top row) and ungulates in areas of low and high human use (threshold human occupancy = 0.54). Nocturnal diel periods (2 hours after sunset to 2 hours before sunrise) are shaded using the average times of sunrise and sunset during our study period, and lighter shading represents the diel-specific nocturnal activity that is different between low and high human areas. Significance levels for bootstrapped randomization test of differences in diel distributions between human zones: * < 0.05, ** < 0.01, *** < 0.001. Plus signs (+) represent species with *p*-values < 0.1 which achieved significance when the human occupancy threshold was adjusted ± 0.1 (Appendix A, Table S2-3).

(+12.3 ± 4.8%), duiker (+7.4 ± 4.4%), bushbuck (+6.9 ± 3.6%), and warthog (+4.5 ± 1.9%); and significant decreases for kob (-5.3 ± 4.2%) and aardvark (-15.0 ± 8.1%; Fig. 2-4). In contrast, 5 ungulate species and all 3 carnivores showed no significant differences in nocturnality. After testing the sensitivity of our results to the human occupancy threshold selected, we found that increasing or decreasing the low vs. high human occupancy threshold by ±0.1 did not alter our interpretation of species' differences in diel activity (Appendix A, Table S2-3). The only change we observed was detecting significance when reducing the threshold from 0.54 to 0.44 for 2 species: African leopard and roan antelope. Our results highlight that most species respond to human occurrence by modifying their behaviours and reducing their realized temporal niche to incorporate more night-time activity, potentially altering predator-prey encounter rates.

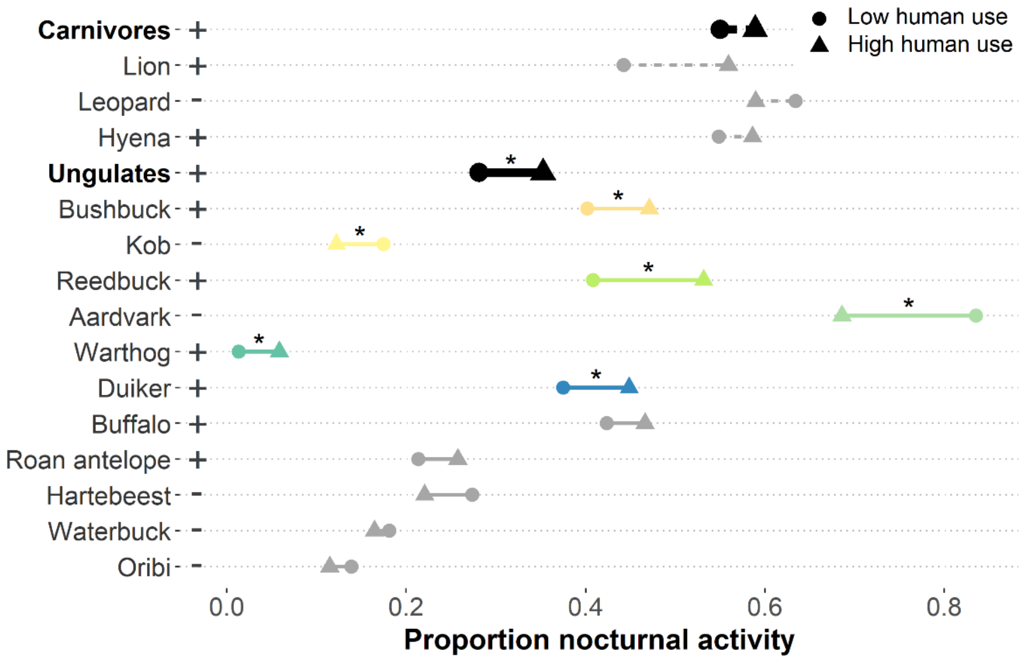

Figure 2-3: Proportion of activity during the nocturnal diel period (2 hours after sunset to 2 hours before sunrise) between low and high human zones for large carnivores (dashed lines) and ungulates (solid lines). Increases and decreases in nocturnality from low to high human use areas are indicated by plus (+) and minus (–) labels next to species' names, respectively. Stars (*) above colored lines indicate species that showed significant differences in nocturnal activity between human zones based on bootstrapped 95% CIs of nocturnality, and the colors of those species' lines correspond to species colors used in Figure 2-5.

Changes in predator-prey overlap

Differences in diel activity among species did not result in significant differences in individual predators' temporal overlap (Δ) with prey when we aggregated their prey species (Appendix A, Fig. S2-2). However, high human use areas showed lower mean overlap of African lions with their prey by 0.08 ($\overline{\Delta}_{\mathrm{high}} = 0.718$ 95% CI ± 0.08; $\overline{\Delta}_{\mathrm{low}} = 0.797 \pm 0.11$). In contrast, African leopards may be experiencing some benefit from human use, as their temporal overlap with prey was 0.17 higher where human activities were high ($\overline{\Delta}_{\mathrm{high}} = 0.699 \pm 0.12$; $\overline{\Delta}_{\mathrm{low}} = 0.529 \pm 0.11$). Spotted hyenas appear to be robust to human occurrence, showing almost no differences in total overlap with prey due to humans ($\overline{\Delta}_{\mathrm{high}} = 0.638 \pm 0.03$; $\overline{\Delta}_{\mathrm{low}} = 0.625 \pm 0.04$).

Human occurrence restructures access to specific prey

African lions and spotted hyenas similarly experienced distinct differences in the composition of accessible prey due to human presence using the 95% CIs of the average difference in percent area under the predator activity curve ($\overline{\Delta}$PAUC), our novel method for assessing predator-prey temporal overlap in a community context (Fig 5a). Specifically, humans generated significant differences in overlap of these predators with 4 out of 11 prey species: bushbuck ($\overline{\Delta}\mathrm{PAUC}_{\mathrm{lion}} = +1.49$ 95% CI ± 1.14%, $\overline{\Delta}\mathrm{PAUC}_{\mathrm{hyena}} = +1.51 \pm 0.73\%$), reedbuck ($\overline{\Delta}\mathrm{PAUC}_{\mathrm{lion}} = +1.99 \pm 1.34\%$, $\overline{\Delta}\mathrm{PAUC}_{\mathrm{hyena}} = +1.88 \pm 0.87\%$), duiker ($\overline{\Delta}\mathrm{PAUC}_{\mathrm{lion}} = +1.56 \pm 1.31\%$, $\overline{\Delta}\mathrm{PAUC}_{\mathrm{hyena}} = +0.84 \pm 0.73\%$), and kob ($\overline{\Delta}\mathrm{PAUC}_{\mathrm{lion}} = -2.24 \pm 1.58\%$, $\overline{\Delta}\mathrm{PAUC}_{\mathrm{hyena}} = -1.45 \pm 0.88\%$) (Fig. 2-5b). All three species to which predator access increased significantly also exhibited increased night-time activity as a human avoidance strategy. In contrast, kob was less active at night in high human areas and experienced lower overlap with lions and hyenas (Fig. 2-4). Additionally, African lion and spotted hyena access to 2 prey species showed near significant differences (buffalo $\overline{\Delta}\mathrm{PAUC}_{\mathrm{lion}} = +1.33 \pm$

1.41%, $\bar{\Delta}\mathrm{PAUC}_{\mathrm{hyena}} = +0.87 \pm 0.97\%$; and waterbuck $\bar{\Delta}\mathrm{PAUC}_{\mathrm{lion}} = -1.66 \pm 1.73\%$, $\bar{\Delta}\mathrm{PAUC}_{\mathrm{hyena}} = -1.67 \pm 1.71\%$).

All three apex predators showed comparable differences in access to all prey between human use levels (Fig. 2-5b). However, differences in African leopard access to prey items were not significant based on 95% CIs, with only aardvark ($\bar{\Delta}\mathrm{PAUC}_{\mathrm{leopard}} = -4.6 \pm 4.7\%$) and bushbuck ($\bar{\Delta}\mathrm{PAUC}_{\mathrm{leopard}} = 1.7 \pm 1.8\%$) access nearing significance (Fig. 2-5). We suspect this is due to leopards' differential response to human presence (-4.6 ± 19.1% change in nocturnality) compared

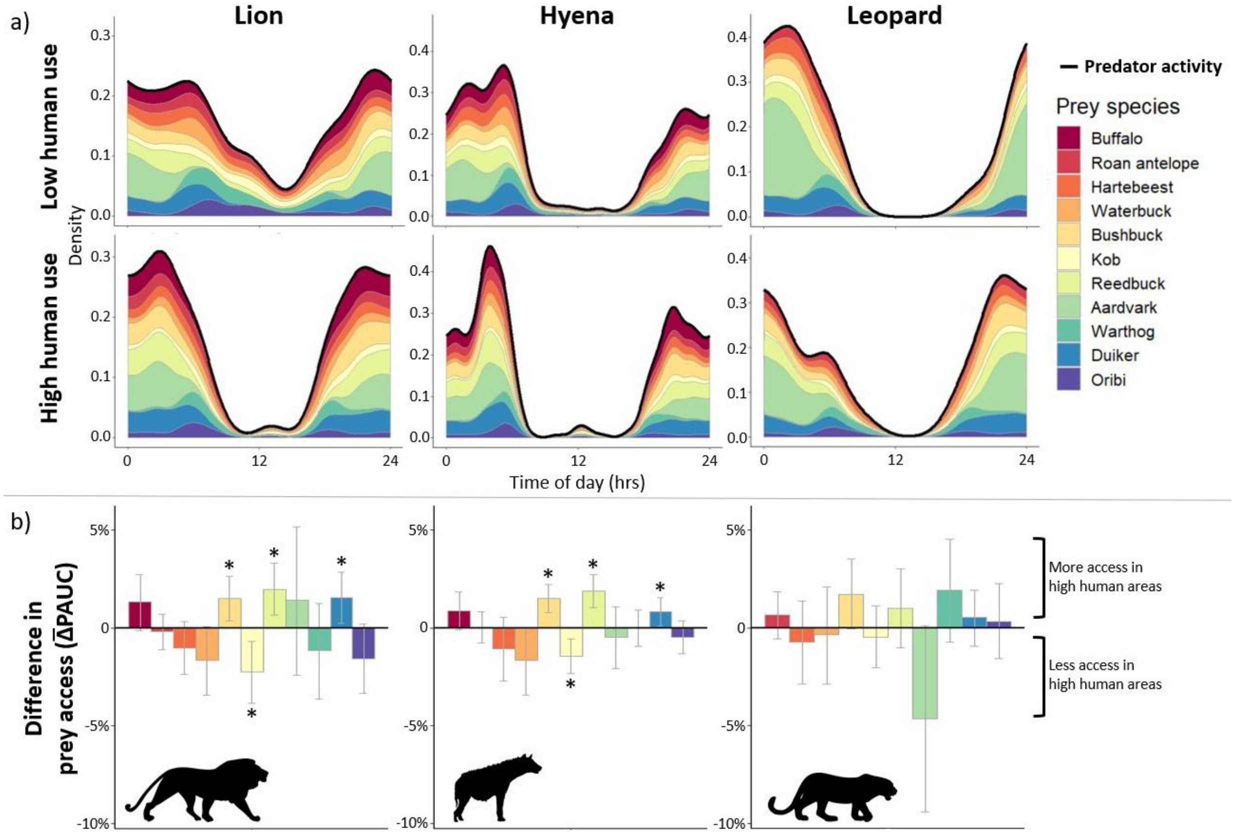

Figure 2-4: Differences in prey access between human activity zones for African lions, spotted hyenas, and African leopards from new temporally explicit community analysis. Buffalo was not included as prey for leopard. a) Temporal overlap heatmaps representing the relative contributions of each prey species to the overall available prey base scaled to predator activity curve (solid black line) over the 24-hour cycle. Density values are calculated from kernel density temporal curves for predators and prey species. b) Mean differences in prey access based on species-specific area under the predator activity curve (ΔPAUC) between areas of low and high human pressure, averaged among 10,000 parametric bootstrap replicates. Error bars represent bootstrapped 95% confidence intervals of $\bar{\Delta}$PAUC, with asterisks (*) designating significant differences in predator access to prey species.

to African lions (+11.9 ± 16.3%) and spotted hyenas (+3.7 ± 6.5%; Fig. 4), though these differences are non-significant.

Although overlap with total available prey did not differ for any predator, human presence increased the variation in species-specific prey accessibility (PAUC estimates) for African lions (Fligner-Killeen test, *p*-value = 0.03), indicating lower diversity of available prey and therefore more access to certain prey species compared to others where human presence was high (Fig. 2-5b). African leopards and spotted hyenas showed no significant differences in access variability as a response to humans.

Discussion

Wildlife responses to human activities have the potential to reshape natural ecological processes and trophic dynamics (Hebblewhite *et al.* 2005; Dorresteijn *et al.* 2015; Suraci *et al.* 2019a). When anthropogenic pressures are heterogeneous, the resultant dynamism promotes a myriad of adaptive strategies to manage and mitigate threats including behavioural shifts in diel activity that redefine species' temporal niches (Muhly *et al.* 2011; Carter *et al.* 2012; Gaynor *et al.* 2018; Frey *et al.* 2020). Such shifts in diel activity may lead to increased prey vulnerability to nocturnal predators, thus altering probabilities of encounter and diets in consumers (Fig. 2-1). We found that over two-thirds of the assessed species exhibited different overall diel activity patterns as a response to humans in the study area. Most species showed more nocturnal activity, consistent with previous works and supporting our hypothesis of human avoidance (Carter *et al.* 2012; Gaynor *et al.* 2018). Valeix *et al.* (2012) and Suraci *et al.* (2019b) similarly found reduced diurnal activity near human settlements in African lions in Makgadikgadi Pans National Park, Botswana, and Laikipia, Kenya, respectively, likely to reduce risks of human encounters. Human presence appears to be limiting temporal refugia from risks for many species and driving increases in ungulate activity when predators are also active, possibly decoupling anti-predator behaviours from predation risks (Dröge *et al.* 2019; Smith *et al.* 2019). Patten *et al.* (Patten *et al.* 2019) also presented evidence of human avoidance driving increased predation risks in North American white-tailed deer (*Odocoileus virginianus*).

Heterogeneity in species' responses to human presence, however, indicates different sensitivities to humans among the carnivores and ungulates in our study system. Some species did not exhibit differences in nocturnality as expected (e.g., kob and aardvark). These species may be benefitting from the observed human avoidance in many sympatric species that potentially reduces risks of predation and competition, commonly referred to as a human shield response (Berger 2007; Muhly *et al.* 2011). For example, Atickem *et al.* (2014) reported mountain nyala (*Tragelaphus buxtoni*) leveraging predator avoidance of humans during the day as a temporal refuge in Ethiopia. The ability to exploit human presence as a shield from predatory or competitive encounters may be due to the life history traits of a species that reduce sensitivity to humans, such as body size, energetic requirements, dispersal abilities, social structure, or foraging strategies (Blumstein *et al.* 2005; Tablado & Jenni 2017). Similarly, these species' temporal niches may be constrained by inherent characteristics that were evolved for diurnal activity, making night-time activity more costly despite refuge from human pressures and limiting their adaptive capacity to avoid humans (Monterroso *et al.* 2013). In contrast, the amount of wildlife persecution (i.e., trophy hunting and poaching) in the system may induce stronger human-avoidance behaviours in hunted species. For instance, Vanthomme *et al.* (2013) attributed the negative associations of 10 mammals with human disturbances in Gabon to hunting avoidance behaviours, contrasted by 6 species in the study showing positive associations. Though the mechanisms driving differential responses to humans were not explicitly investigated here, our study demonstrates non-uniform responses of large mammals to human presence. As such, future work can assess the drivers of species-specific responses and sensitivities to humans.

We showed that human presence modified the availability of prey species relative to the overall pool of available prey, which is an important driver of prey selection in apex predators, and thus provide new insights into community-level repercussions of human sympatry with wildlife (Sinclair *et al.* 2003; Owen-Smith & Mills 2008). While we expected overall predator-prey overlap and the diversity of available prey to be higher due to human avoidance, the combination of human avoidance and human shield strategies observed in our system resulted in little difference in overall overlap but substantial differences in apex predator access to individual prey species. Specifically, our new community-level approach to predator-prey temporal overlap revealed that prey species experienced intensified overlap with predators when they increased their nocturnal temporal niche (e.g., duiker, reedbuck, bushbuck) to avoid humans, while overlap was lessened for species that did not (e.g., kob). For African lions, this resulted in a lower diversity of available prey, likely intensifying predation pressures on a smaller subset of species which could contribute to destabilizing trophic dynamics (Gross *et al.* 2009). This highlights increasing concerns for the persistence of the now Critically Endangered West African lions that are suffering from prey depletion (Henschel *et al.* 2014). The predators in our study are largely opportunistic night-time hunters, and temporal overlap is often strongest between predators and their preferred prey species (Hayward & Slotow 2009; Linkie & Ridout 2011; Ramesh *et al.* 2012; Dou *et al.* 2019). Thus, we expect that species experiencing the highest overlap with apex predators relative to other prey to be integrated into the predators' diets in higher proportions, and consequently expect varied prey selection by predators between low and high human use areas. Buffalo are a common prey item of African lions in other systems, and our results suggest they may be vulnerable to intensified selection by lions due to human presence increasing access to buffalo in our study area (Davidson *et al.* 2013). Our approach implemented in this study may therefore be useful for anticipating herbivore population declines as a result of intensified predation pressures, as well as potential resulting feedbacks into predator population stability especially for endangered species such as the West African lion (Owen-Smith *et al.* 2005). Additionally, human disturbance can increase the predation rates and carcass abandonment by large carnivores as well as alter mesopredator foraging behaviours, potentially increasing mortality rates on preferred prey species and providing augmented carrion resources that may be detrimental to scavenger populations (Smith *et al.* 2015; Prugh & Sivy 2020). As such, disturbances to predator-prey relationships potentially lead to alterations in predators' diets with consequences for ungulate and mesopredator community regulation and nutrient distribution (Schmitz *et al.* 2010; Owen-Smith 2019).

Though protected areas are the primary strategy for biodiversity conservation worldwide, human exploitation of protected areas is pervasive and in many cases necessary for the sustenance of human populations (Jones *et al.* 2018; Geldmann *et al.* 2019). By accounting for imperfect detection to understand human space use, we contribute to a more comprehensive understanding of human impacts within coupled human-natural ecosystems that is imperative to effectively manage for the conservation of ecological processes, biodiversity, and human needs. However, human activities observed in our study system may not impact species uniformly. Because we aggregated a variety of human activities to depict human use, there might be activity-specific responses by wildlife that were not captured. Humans exploit resources in national parks in many ways including livestock herding, resource gathering, subsistence poaching, hunting, and recreation, all of which impact the system and wildlife to varying degrees (Everatt *et al.* 2019; Geldmann *et al.* 2019; Harris *et al.* 2019). Indeed, Harris *et al.* (2019) found differential impacts of human activities on wildlife behavior in WAP, suggesting species in this system do not respond to all humans uniformly. However, limited sample sizes of many human activity categories currently preclude more detailed analyses using an occupancy framework. Overall, human impacts encompass a variety of disturbances that impact ecosystems, both in our study and more broadly, and thus disentangling the responses of wildlife to specific human pressures may facilitate designing more effective conservation interventions (Jones *et al.* 2018; Nickel *et al.* 2020). Our results are also suggestive of the potential ecological effects of changes to human activity in natural areas, which could result from fluctuations in tourism, infrastructure development, policy changes, and other local or global processes.

Our results demonstrate prevalent disruptions to wildlife temporal activity patterns from human presence, leading to overall reductions in diurnal activity and modified community dynamics. Because both carnivores and ungulates serve fundamental roles in regulating African ecosystems via predation and herbivory, respectively, the pervasiveness of their responses to human occurrence demonstrates the capacity for humans to disrupt essential ecological processes that facilitate coexistence among wildlife, in this case reshaping predator-prey interactions. As the human footprint continually expands, spatial refugia from anthropogenic disturbance become more limited, stimulating an increasing need to exploit temporal partitioning to avoid human pressures. We show that the community-level implications of these behavioural modifications must be considered in light of complex higher-order interactions that govern mechanisms of coexistence among predators and their prey.

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Chapter III

Tradeoffs Between Resources and Risks Shape Large Carnivore Responses to Human Disturbance

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Abstract

Wide-ranging carnivore species experience tradeoffs between dynamic resource availabilities and heterogeneous risks from humans, with consequences for their ecological function and conservation outcomes. Yet, research investigating these tradeoffs across large carnivore distributions is rare. We assessed how the strength of lion (*Panthera leo*) responses to disturbance is influenced by resource availability and anthropogenic risks using data from 23 studies at 31 sites, spanning 40% of lions' contemporary range. Lions avoided human disturbance at over two-thirds of sites by decreasing space use or increasing nocturnal activity, though their responses varied widely depending on site-level characteristics. Lions were more likely to exploit human-dominated landscapes where resources were limited or inconsistent, indicating that resource limitation can outweigh anthropogenic risks and might exacerbate human-carnivore conflict as

climates change. Lions also avoided humans by increasing their nocturnal activity more often at sites with higher production of cattle, signaling the pervasive ecological impacts of livestock production. By limiting the spatiotemporal niches of large carnivores, the global expansion of human impacts threatens to downgrade their ecological function across a range of environmental conditions. Expected declines in resource availability are also likely to intensify human-carnivore conflicts, escalating extinction risks for many threatened species.

Introduction

Humans and wildlife are increasingly sharing the world's landscapes and interacting at an unprecedented scale (Jones *et al.* 2018; Ellis 2019; O'Bryan *et al.* 2020). Wildlife responses in these shared landscapes determine both their survival and their roles in the evolving social-ecological systems that govern human and wildlife livelihoods (Ostrom 2009; Carter *et al.* 2014; Dirzo *et al.* 2014; Dressel *et al.* 2018). Ongoing global environmental changes and growing human pressures (e.g., expanding agricultural lands) are likely to further intensify wildlife responses to humans. Altered wildlife and human distributions, behaviors, and interactions have the potential to escalate human-wildlife conflicts and increase extinction risks for many species (Tucker *et al.* 2018; Guiden *et al.* 2019; Manlick & Pauli 2020; Merkle *et al.* 2022; Abrahms *et al.* 2023). Understanding the complexities of the spatiotemporal responses of wildlife to human disturbance is a key first step in identifying the conditions necessary to foster socioecological coexistence between humans and wildlife (Carter & Linnell 2016).

In human-dominated landscapes, wildlife must balance the tradeoffs between resource acquisition and the potentially lethal risks of human encounters (Darimont *et al.* 2015; Loveridge *et al.* 2017; Nickel *et al.* 2021). This is particularly true for large carnivores when they target livestock as prey because threats to livestock often prompt retaliatory killing of large carnivores, a leading cause of large carnivore decline worldwide (Ripple *et al.* 2014; Darimont *et al.* 2015). The flexible spatiotemporal behaviors of large carnivores allow them to hunt prey while reducing harmful interactions with other predators or humans (Cozzi *et al.* 2012; Bennie *et al.* 2014; Dröge *et al.* 2017; van der Vinne *et al.* 2019; Mills & Harris 2020). Some large carnivores exploit this flexibility to alter their activity patterns and space use in response to risks from humans, although these changes may come with fitness consequences or restructure ecological processes (Frid &

Dill 2002; Gaynor *et al.* 2019). For example, many carnivore species avoid human encounters by being active mostly at night, referred to as temporal avoidance (Carter *et al.* 2012; Gaynor *et al.* 2018), which can influence interspecific competition, predator-prey dynamics, and ecosystem function (Cozzi *et al.* 2012; Kohl *et al.* 2019; Cox *et al.* 2022). Carnivore species can also avoid human-dominated areas altogether via spatial avoidance, which effectively limits their available habitat and can increase competition, contribute to heightened extirpation risks, restructure community dynamics, and reduce biodiversity (Ripple *et al.* 2014; Šálek *et al.* 2015; Enquist *et al.* 2020; Kotze *et al.* 2021).

Heterogeneity in risk-averse behaviors among species is well-documented (Geffroy *et al.* 2015; Frey *et al.* 2020; Suraci *et al.* 2021), but it is unclear how widespread these behaviors are within a given carnivore's distribution. We also lack empirical insights on the mechanisms shaping these behaviors across gradients of anthropogenic disturbance and ecological conditions. For example, resource scarcity could prompt predators to expand their realized spatial or temporal niches to meet their metabolic needs at the expense of their safety (Gittleman & Harvey 1982; Macdonald 1983; Loveridge *et al.* 2009; Hirt *et al.* 2021). Varying intensity and types of human disturbance within a species' range – such as spatially static infrastructure and land use versus temporally dynamic human presence – can also moderate risk-averse behaviors, even leading to the habituation of wildlife to humans in some cases (Schell *et al.* 2018; Nickel *et al.* 2020). Range-wide syntheses of large carnivore responses to disturbance are therefore needed to better understand their ecology and conservation in shared, complex landscapes (Ripari *et al.* 2022).

We investigated the spatiotemporal responses of lions (*Panthera leo*) to human disturbances across their range. Almost half of the current range of lions lies outside of protected area boundaries, requiring lions to regularly navigate degraded human-dominated landscapes

(IUCN SSC Cat Specialist Group 2018; Robson *et al.* 2021; Loveridge *et al.* 2022). Accelerating human population growth across Africa (particularly near protected areas) and expanding agricultural lands will intensify the human-lion interface and potential conflicts due to livestock depredation (Thuiller *et al.* 2006; Wittemyer *et al.* 2008). The additional stressors of ongoing prey depletion (Wolf & Ripple 2016; Lindsey *et al.* 2017) and climate changes (Hulme *et al.* 2001; Dixon *et al.* 2003) are expected to exert unprecedented pressures on lions and other wildlife in coming years. Although lions have been extensively studied, large-scale patterns in lion responses to humans remain unclear and are clouded by heterogeneous results among lion populations.

To investigate how lions navigate shared landscapes, we conducted a meta-analysis that examines lion spatiotemporal responses to human disturbance over gradients of disturbance intensity and resource availability. By synthesizing the impacts of human disturbance on large carnivore niche space, we improve our ability to predict how continued human development and global environmental change will impact wildlife behaviors and ultimately their survival. Specifically, we examined whether 1) lions avoid the risks of human disturbance on average across sites by exhibiting lower space use and more nocturnal activity in areas of high disturbance (i.e., reducing spatiotemporal overlap with disturbance); 2) lions exhibit stronger human avoidance behaviors at sites with higher overall human disturbance, including livestock production; and 3) lion avoidance of human disturbance is mitigated by variable primary productivity that likely limits wild prey availability.

Through a systematic literature review, we compiled lion occurrence and activity data from 23 studies, representing 31 independent study sites that span 40% of the contemporary range of lions (Riggio *et al.* 2013) from expansive protected areas to subsistence agricultural lands. We assessed the strength of lion responses to human disturbance at each site by comparing the intensity of space use and/or the proportion of nocturnal activity between treatments of low and high human disturbance. We quantified effect sizes for lion responses to disturbance using the standardized mean difference (SMD) for spatial responses and the log-response ratio (RR) for temporal responses. We used meta-analytic mixed-effects models to calculate the average effect size for lion responses across studies, weighted by study variance (SMD_w and RR_w), as well as investigate the impacts of site-level anthropogenic and environmental conditions on the strength of lion responses to disturbance. We extracted the average and spatial variation of the Human Footprint Index (Keys *et al.* 2021) (HFI) at each study site to represent a comparable measure of the intensity and spatial heterogeneity in human disturbance across sites. We also compared lion responses to disturbance with the intensity of livestock production at each site (Robinson *et al.* 2014). To assess the effects of resource availability on lion avoidance of disturbance, we used satellite-derived measures of vegetation greenness (i.e., Normalized Difference Vegetation Index [NDVI]) that correlate directly with primary productivity and wild prey abundances (Pettorelli *et al.* 2009; Borowik *et al.* 2013; Fløjgaard *et al.* 2021), including the overall average NDVI during the study period as well as spatial and temporal variability in NDVI. Characteristics of the studies used in the meta-analysis (such as the lion observation method, human disturbance measures, or study area size) were also tested for their influence on observed lion responses to ensure that heterogeneity in study design across sites did not unduly influence our results.

Methods and Materials

Literature Search

We conducted a systematic literature search for peer-reviewed published studies using the ISI Web of Science (WoS) database on lion spatiotemporal activity patterns in relation to human disturbances (Koricheva *et al.* 2013; O'Dea *et al.* 2021). We also searched for unpublished studies and datasets using the ProQuest Dissertations & Theses database and the Dryad Digital Repository. On WoS and ProQuest, the following Boolean search strings were used: ("Panthera leo" OR "African lion" OR "Lion") AND ("human" OR "anthropogenic") AND ("Avoid*" OR "Space use" OR "Spatial" OR "Respon*" OR "Behavior" OR "temporal" OR "diel" OR "Land use" OR "Management"). We filtered our search for articles (WoS) and dissertations/theses (ProQuest) that fell into the relevant subject categories (e.g., ecology, environmental science, biodiversity conservation) and were published between 1990 and 2021. To expedite the review process, we also excluded results that included terms such as 'mountain lion', 'pinniped', 'tamarin', or 'primate' in the abstract or title, as these were common topics in studies returned from the search that were not relevant to our meta-analysis (exact search strings for each database can be found in Appendix B). We broadened our dataset by searching the titles of literature cited in each of the included publications (i.e., a snowball approach). Because some studies collected lion activity data but did not report results relevant to this meta-analysis or publish their raw data, we also contacted authors and requested unpublished data to reduce publication bias.

Inclusion criteria

We screened the search results first by title, then by abstract, and finally by reading the full text and supplemental materials. We began by including any study with a title that was related to large carnivores, African wildlife, and/or anthropogenic pressures. We then screened the abstracts of the remaining publications, including those that appeared to measure the activity of large African mammals — or lions specifically — and that might reasonably include considerations of human disturbance in the study. In our final dataset, we included any study that measured lions' spatial or temporal activity across spaces or times of varying human disturbance, enabling a calculation of means and standard deviations of lion activity levels between dichotomous control (low disturbance) and treatment (high disturbance) designations.

Lion spatiotemporal activity was measured by camera traps, VHF or GPS telemetry, or direct observation. We considered studies that measured human disturbance with metrics representing direct human activity or infrastructure (e.g., human detections on camera traps, distance to villages). We also included studies that did not measure human disturbance but provided georeferenced data on lion activity that could be compared to available human disturbance data (Human Footprint Index [Keys et al., 2021]). When a given dataset of lion spatiotemporal activity was published in multiple studies, we selected the study which provided the most comprehensive and recent version of the dataset.

Extraction of lion spatiotemporal data

For each study or dataset, we calculated the average measure of lion space use (e.g., occupancy estimates, camera trap success, density of observations, or GPS fixes) and/or the proportion of active (i.e., not resting) nocturnal observations (P) between designations of low and high human disturbance within the study site (Appendix C, Fig. S3-2). In cases where direct observation surveys of lions occurred primarily during the daytime (n = 3), we excluded these studies from calculations of the proportion of nocturnal activity and spatial responses may be biased towards daytime lion activity. We defined nocturnal activity as observations of lion activity that occurred when the sun was lower than six degrees below the horizon unless otherwise specified by the study text (Signer *et al.* 2019). Solar positions were calculated for the time of each lion observation and the specific sample unit coordinates, when available, or the survey site centroid. If the exact site coordinates were not provided by the authors, we estimated the approximate latitude and longitude of the site centroid using site descriptions, figures and maps from the original publications, and Google Maps. To identify ‘active’ observations in GPS telemetry datasets, we used the sequential clustering algorithm in the ‘GPSeqClus’ R package (Clapp *et al.* 2021) to identify ‘clusters’ of more than 2 lion GPS locations given a 100-m search radius and temporal window of 2 days. We considered ‘clusters’ of GPS fixes to represent lion inactivity that were excluded from our analyses, designating the remaining GPS fixes as active observations that were used to calculate nocturnality. Similarly, we considered all independent camera trap detections to represent active observations. Additional descriptions of data extraction methods can be found in Table S2.

Quantifying human disturbance

Designations of human disturbance at the lion observation level (used to calculate effect sizes) were derived in one of two ways depending on the study site and survey design. 1) We used disturbance metrics provided by the study data which we classified as representing infrastructure (such as the distance of observations from villages) or direct human activity (such as humans captured on camera traps). 2) For studies that did not provide disturbance data, we extracted the Human Footprint Index (Keys *et al.* 2021) at georeferenced lion observation locations. The human footprint index (HFI) is a global dataset (~10-km resolution) that aggregates various axes of human impacts on ecosystems (e.g., population size, infrastructure, agriculture, etc.) into a single index of human pressure, and we thus categorized it as representing both infrastructure and direct human activity (Keys *et al.* 2021). Both approaches were used to identify locations or times that experienced low versus high levels of disturbance that could be assigned to measurements of lion activity. Low and high disturbance designations could represent discrete periods of time or land units (e.g., land use types or management blocks), or a continuous mosaic of human disturbance (e.g., distance to a village) that could be binned into low and high disturbance categories. In studies with a continuous mosaic of human disturbance, we extracted the value of the human disturbance metric for each spatial sampling unit (e.g., camera station or grid cell). For datasets consisting of lion GPS fixes without clear spatial sample units, we used the average daily displacement distance ($\bar{\delta}km$) of lions to create a $\bar{\delta}km^2$ grid across the study site to serve as the sample units within which observations were aggregated for subsequent analyses. If $\bar{\delta}km^2$ could not be calculated, such as for direct observation studies, we used a 1-km^2 grid. We used a power analysis of a two-tailed t-test to guide our selection of cutoff values to assign low and high disturbance, which indicated that approximately 60 samples or more per group were required to achieve 80% power to detect differences in means. For each study site, we assigned the 1st and 3rd quartiles of the human disturbance variable as cutoff values for low and high disturbance categories, eliminating noise generated by intermediate levels of disturbance. However, if the number of sample units in each quartile was <60 for a given site, we instead used the median value of disturbance at that site as the cutoff value (Table S2).

Effect sizes

To evaluate the effects of human disturbance on lion activity, we calculated the standardized mean difference (SMD) and log response ratio (RR) of lion space use and nocturnality, respectively, between low and high human disturbance treatments at each study site using the '*metafor*' R package (Viechtbauer 2010; Koricheva *et al.* 2013). In determining spatial responses, we calculated SMD using Hedge's *d* metric of effect size (Hedges & Olkin 1985; Koricheva *et al.* 2013). When SMD < 0, human disturbance negatively impacted lion space use, indicating human avoidance behaviors, while SMD > 0 conversely indicated more use of high disturbance areas. We similarly calculated the log response ratio of temporal responses using:

$$RR = \ln\left(\frac{P_{low}}{P_{high}}\right)$$

Equation 3-1: Calculation of the log-response ratio for lion nocturnality between low and high disturbance treatments

in which P_{low} and P_{high} represent the proportion of active lion observations that occurred during nocturnal hours in low and high human disturbance areas. Higher levels of lion nocturnality in response to human disturbance are signified by RR < 0, while RR > 0 indicates more diurnal activity in high-disturbance areas. Increased nocturnal activity in high disturbance treatments is assumed to be an avoidance response in large carnivores, as human activity is usually concentrated during daylight hours (Carter *et al.* 2012; Gaynor *et al.* 2018; Mills & Harris 2020). We also report the back-transformed RR to calculate the percent by which lions increased their nocturnality due to human disturbance. We calculated the variance of RR for each study as follows (Koricheva *et al.* 2013), where n indicates sample sizes of lion observations in low and high human disturbance areas:

$$Variance_{RR} = \frac{(1 - P_{low})}{n_{low}P_{low}} + \frac{(1 - P_{high})}{n_{high}P_{high}}$$

Equation 3-2: Calculation for variance of the log-response ratio for lion nocturnality

Spatial variables

We considered three site-level spatial variables across all of the study sites that might influence the strength of lion responses to within-site human disturbance (i.e., the magnitude of meta-analysis effect sizes): 1) cattle production, 2) human footprint, and 3) primary productivity. We created a circular buffer around the geographic centroid of each study site (hereafter, the buffered study area) within which we extracted and summarized the 3 site-level spatial variables. To assess the sensitivity of our analyses to buffer size selection, we compared two buffer methods:

one with the buffer area equal to the study area size specified by the study authors (study-specific buffer area), and another applying the minimum study area size to the buffer of all sites (uniform buffer area). The two methods were compared using univariate model selection, as described in the 'Meta-regression and statistical analyses' section.

We calculated the average cattle production (CAT_a) within each circular buffered study area using a dataset that estimates global cattle production (~10-km resolution) (Gilbert *et al.* 2018). We then used the human footprint index to assess the overall human pressure at each site (Keys *et al.* 2021). Because this dataset provides HFI estimates in 2000 and 2019, we extracted the site-level HFI data for the year closest to the median date of each lion survey dataset. We expected that the overall level of human pressure as well as the existence of spatial refugia from those pressures might influence lion habituation, and thus their avoidance behaviors, so we calculated the average (HFI_a) and the coefficient of variation (CV) of HFI (HFI_{sp}, representing spatial variation in HFI) within each buffered study area. Finally, we used the Normalized Difference Vegetation Index (NDVI) time series dataset provided by MODIS Land Products data (250-m resolution) to summarize primary productivity for each study, thereby accounting for environmental changes and the forage quality for herbivore prey (Pettorelli *et al.* 2009; Fløjgaard *et al.* 2021). Though the correlation between primary production and wild prey availability may be decoupled in protected areas experiencing large-scale defaunation in recent decades (Craigie *et al.* 2010), we chose to include NDVI in our study as the closest proxy available for broad-scale patterns in site-level wild prey availability. We obtained NDVI layers for the 1st day of each month from January 2000 (the earliest available date) to September 2019 (the latest date of a lion survey) using the '*MODIStsp*' R package (Busetto & Ranghetti 2016). We calculated 3 metrics of NDVI at each site, where μ_i and σ_i are the average and standard deviations of all NDVI pixels within the buffered study area for month i:

1) the overall mean monthly NDVI across months (**Equation 3-3**),

$$NDVI_a = \frac{1}{n}\sum_{i=1}^{n} \mu_i$$

2) the average within-month CV of NDVI (representing mean spatial variation in productivity, **Equation 3-4)**,

$$NDVI_{sp} = \frac{1}{n}\sum_{i=1}^{n} \frac{\sigma_i}{\mu_i}$$

and 3) the CV of mean monthly NDVI (representing temporal variation in mean monthly productivity, **Equation 3-5**),

$$NDVI_{tm} = \frac{\sqrt{\frac{\sum(\mu_i - NDVI_a)^2}{n}}}{NDVI_a}$$

Because lion responses to humans could be influenced by long- and short-term patterns in site-level ecosystem productivity that influence wild prey abundances, we compared the sensitivity of our analyses to the temporal scale of NDVI layers used in calculating these metrics. Thus, the 3 metrics were calculated at each study site once using the entire January 2000-September 2019 monthly NDVI dataset (long-term) and again using only the months in which each lion study took place (short-term). The two temporal ranges for NDVI metrics were compared using univariate model selection, as described in the ‘Meta-regression and statistical analysis’ section. All spatial variables were scaled and centered to produce standardized model coefficients in the statistical analyses, allowing for comparisons among variable effects on lion responses to human disturbance. We also assessed the correlation among all of the spatial variables to ensure that highly correlated variables ($r > 0.6$) were not included together in statistical models. To support our inference of NDVI as a metric for climatic trends, we also extracted monthly rainfall estimates for each study site (excluding 2 sites in India due to data availability) from TAMSAT precipitation data (Maidment *et al.* 2017) for Africa (2000-2019) and created a linear model which compared the effects of average precipitation on average NDVI per month for each study site (i.e., a site:rainfall interaction term). Because the two variables are highly correlated (Appendix C, Table S3-4, Fig. S3-2) and NDVI more directly influences wild prey availability for lions (Pettorelli *et al.* 2009; Fløjgaard *et al.* 2021), we did not include precipitation data in subsequent analyses.

Meta-regression and statistical analysis

For studies that measured both response types, we modeled spatial effect sizes as a function of temporal effect sizes using a linear model to assess the existence of spatiotemporal tradeoffs in human avoidance behaviors. We then assessed how the heterogeneity in lion responses to human disturbance among studies (i.e., the effect sizes) was influenced by the metrics calculated from the three spatial variables using separate mixed-effects models for spatial and temporal lion responses (with the study ID as a random effect). We weighted the studies using the inverse of their calculated sampling variance and used the maximum likelihood estimation of residual heterogeneity. The intercept term of the generated models was interpreted as the average weighted effect size of human disturbance on lion responses (SMD_w or RR_w). We used the Akaike Information Criterion corrected for small sample sizes (AIC_c) to compare models and identified the model with the lowest AIC_c as the best performing model during model selection. All models were built and assessed using the '*metafor*' package in R (Viechtbauer 2010).

We first compared the performance of each spatial variable calculated using the two buffer sizes (all spatial variables) and two temporal ranges (for NDVI) by creating and comparing univariate mixed-effects models. The metric included in the lowest AIC_c model for each spatial variable metric (e.g., HFI_{sp}) was then chosen to be included in the global model. If the models did not differ by > 2 ΔAIC_c, then we used the metrics calculated based on the site-specific study area size and study period. Our results were robust to the selection of buffer size or temporal range of NDVI data except for one case in which the minimum buffer size offered marginally higher explanatory power for temporal responses to spatial variation in primary productivity ($NDVI_{sp}$, $\Delta AIC_c = 2.19$). We then compared mixed-effects models using all combinations of the 6 spatial variable metrics included in the global model (SMD or RR ~ $CAT_a + HFI_a + HFI_{sp} + NDVI_a + NDVI_{sp} + NDVI_{tm}$). We present models with $\Delta AIC_c < 2$ compared to the best. We used the standardized variable coefficients from the lowest AIC_c model to assess variable effects. Mixed-effects models with small sample sizes can result in inflated and unreliable values of common model evaluation metrics (López-López *et al.* 2014; Von Hippel 2015), such as $\hat{\tau}^2$, I^2, and R^2, which estimate the amount of heterogeneity in the true effect sizes, the proportion of variability attributed to heterogeneity among the true effect sizes, and the amount of heterogeneity explained by model variables, respectively. We thus evaluated the performance of the mixed-effects models at explaining heterogeneity in lion responses using the 95% confidence intervals of the I^2 and $\hat{\tau}^2$ measures, rather than the precise point estimates, as well as the Q_E-test for residual heterogeneity. Finally, we assessed whether study characteristics — including the type of human disturbance measured to calculate effect sizes (e.g., infrastructure versus direct activity), whether the study site is fenced, lion observation method, study area size, study season, study duration, and median study date — might influence the observed effect sizes using ANOVA tests for categorical variables and linear models for continuous variables.

Results

Avoidance of human disturbance

We identified 31 total study sites from 492 search results, resulting in 30 estimates of spatial responses and 18 estimates of temporal responses by lions to humans (Fig. 3-1). Lions tended to avoid within-site human disturbance with lower space use ($SMD_w = -0.268$, 95%CI ± 0.165) and a 7.08% (95%CI 3.34 to 10.94%) increase in nocturnal activity in high disturbance areas of a given site ($RR_w = -0.068$, 95%CI ± 0.035) (Fig. 3-2a). There was high heterogeneity in effect sizes for spatial responses among studies (τ^2 95%CI: 0.108, 0.449; I^2 95%CI: 82.2, 95.0%), and somewhat lower heterogeneity (as well as lower confidence in heterogeneity estimates) in lion temporal responses among studies (τ^2 95%CI: 0.006, 0.251; I^2 95%CI: 66.7, 98.7%). We extracted

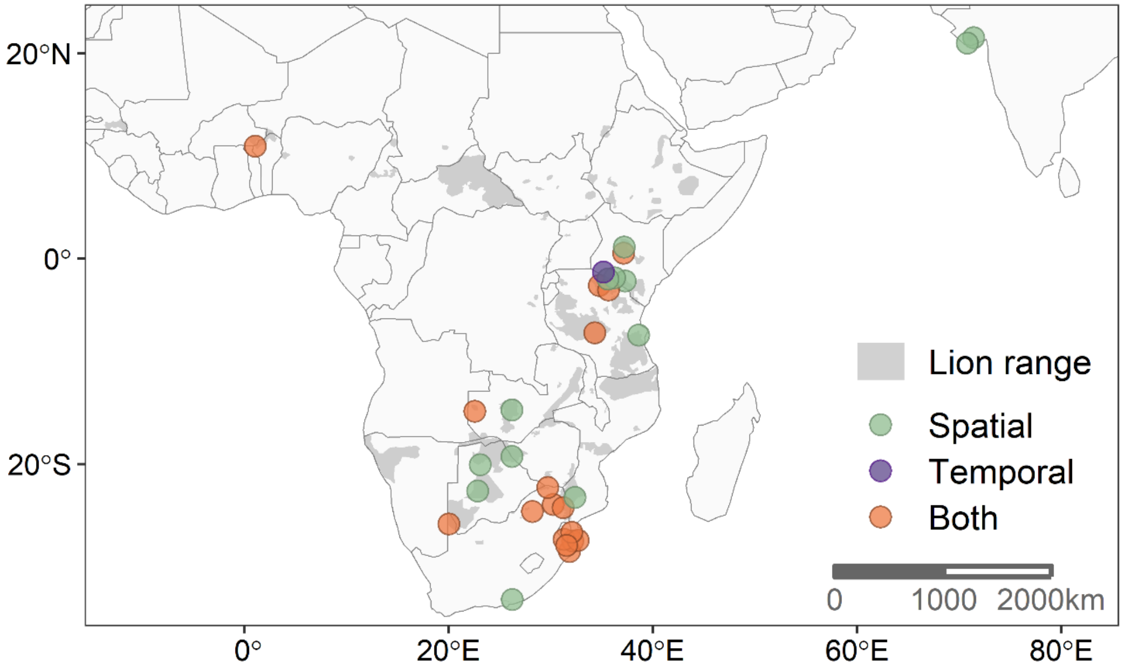

Figure 3-1: The geographic distribution of study sites (n = 31) included in the meta-analysis across the current extant range of lions (estimated by the IUCN). Colors of points indicate which type of response was calculated for each study site (spatial only [green], temporal only [purple], or both [orange]). Points are not precisely representative of study area centroids to reduce overlap of nearby points (e.g., the positions of two points for studies in Gir National Park, India, are slightly adjusted so that both are visible). Map lines delineate study areas and do not necessarily depict accepted national boundaries.

both spatial and temporal effects of human disturbance on lion activity for 17 study sites. Across those sites, there was no relationship between the magnitude of spatial and temporal responses ($\beta = -0.415$ [SE 0.28], $R^2 = 0.12$, $F = 2.138$, $df = 15$, $p = 0.16$; Fig. 3-2b).

Ecological and anthropogenic conditions

The best mixed-effects models revealed substantial effects of NDVI patterns on the strength of lion responses to human disturbance within each site. Lions were more likely to reduce spatial overlap with high disturbance areas in sites where there was high spatial variation in site-level NDVI ($NDVI_{sp}$: $\beta = -0.893$, 95%CI ± 0.221; Fig. 3-3b), as well as more consistent NDVI over time ($NDVI_{tm}$: $\beta = 0.218$, 95%CI ± 0.184; Fig. 3-3e). Primary productivity may also influence the strength of lion temporal responses, as we observed stronger nocturnal shifts at sites with high average NDVI ($NDVI_a$: $\beta = -0.015$, 95%CI ± 0.013; Fig. 3-3d) and high spatial variation in NDVI

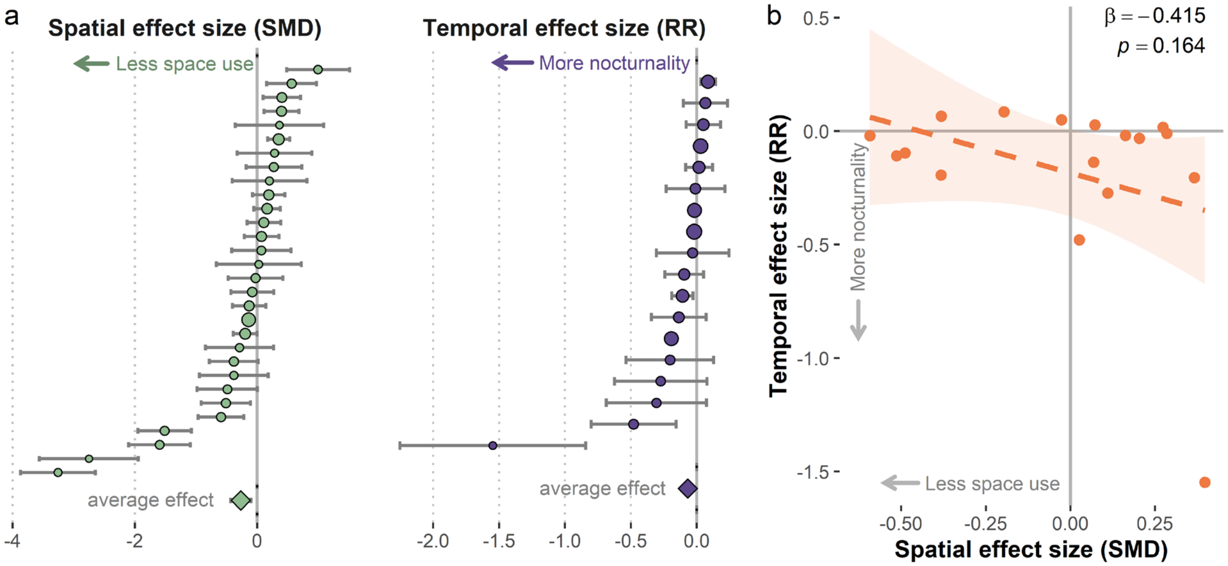

Figure 3-2: The effects of human disturbance on lion space use and nocturnality across all 31 study sites. Negative effect sizes indicate lion avoidance of high human disturbance domains at a given study site (e.g., lower space use or higher levels of nocturnal activity). a) Forest plots of lion spatial responses (SMD = standardized mean difference, n = 30) and temporal responses (RR = log response ratio, n = 18) among all studies with 95% CI. Studies are organized in descending order of effect size, and point sizes are proportional to the inverse variance used to weigh each study. Diamond shaped points depict the average weighted effect (SMD_W and RR_w) of both response types. b) The relationship between spatial and temporal effect sizes for study sites where both responses could be extracted (n = 17). The outlier point in the bottom right corner of the plot is discussed in the "Results" section.

(β = -0.061, 95%CI ± 0.016; Fig. 3-3b). As expected, monthly NDVI and precipitation were positively correlated at 28 of 29 African study sites included in the meta-analysis (Fig. S3-3;

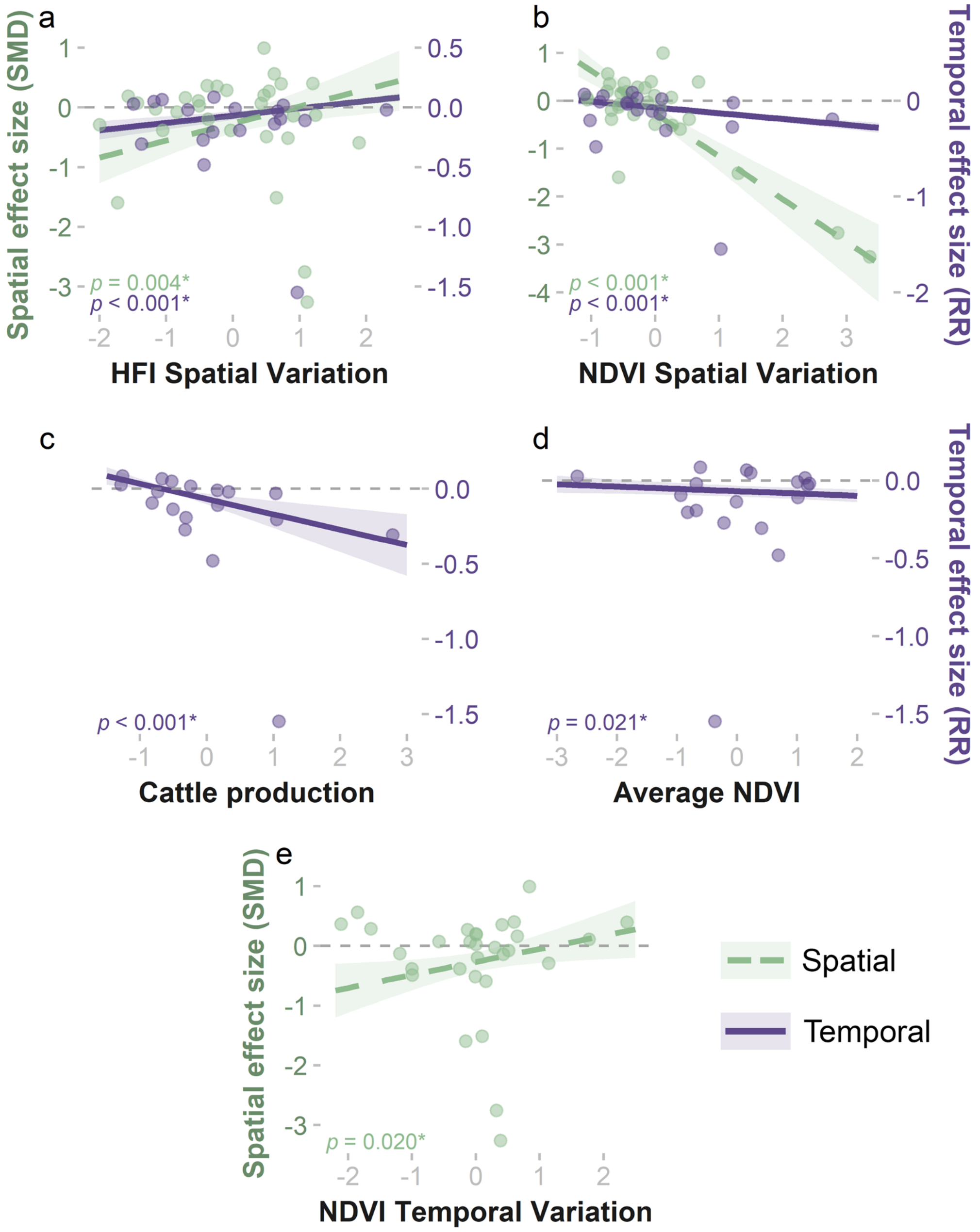

Figure 3-3: The effects of site-level ecological conditions and anthropogenic disturbance on lion spatial (green dashed line, left y-axis) and temporal (purple solid line, right y-axis) responses. Plots a-e depict results from the lowest AIC$_c$ mixed-effects models for both types of responses: a) spatial variation in the Human Footprint Index (HFI_{sp}); b) spatial variation in NDVI ($NDVI_{sp}$); c) cattle production (CAT_a); d) average overall NDVI ($NDVI_a$); and e) temporal variation in NDVI ($NDVI_{tm}$). Linear fits represent the estimated model coefficients with 95% CIs (see Table S3 for variable coefficients). All variables are scaled and centered, and all significantly affected the magnitude of lion responses to human disturbance (p < 0.05). Negative values on both y-axes suggest lion avoidance of human disturbance in time and space. SMD = standardized mean difference; RR = log response ratio.

Appendix C, Table S3-4), confirming that ecosystem productivity was in part dictated by climate trends and usually increased during rainy months.

Site-level variation in human pressure also influenced how lions responded to human disturbance within each site. Lions avoided high disturbance areas both spatially and temporally where there was low spatial variation in overall human pressure (HFI_{sp}: $\beta_{\text{spatial}} = 0.286$, 95%CI ± 0.194; $\beta_{\text{temporal}} = 0.061$, 95%CI ± 0.022; Fig. 3-3a). Lions also exhibited shifts towards more nocturnal behavior in response to human disturbance at sites with high levels of cattle production ($\beta = -0.102$, 95%CI ± 0.058; Fig. 3-3c). However, tests for residual heterogeneity in both the spatial ($Q_E = 143.99$, $df = 26$, $p < 0.001$) and temporal models ($Q_E = 38.53$, $df = 13$, $p = 0.002$) suggested that additional unexplored variables may influence the strength of lion responses.

Study characteristics

The responses of lions to direct human activity versus infrastructure did not differ (spatial responses: $F = 0.72$, $df = 2$, $p = 0.49$; temporal responses: $F = 1.54$, $df = 2$, $p = 0.25$; Appendix C, Fig. S3-4). Similarly, none of the other assessed study characteristics (i.e., lion observation method, study area size, study season, study duration, and median study date) influenced the observed effect sizes for the spatial responses of lions (Appendix C, Figs. S3-4 & S3-5). In contrast, the strength of the shifts in lion nocturnal activity appeared to change over time and depended on the observation method used. Lions were less likely to use (or researchers were less likely to observe) increased nocturnality to avoid humans in studies conducted in later years ($F = 20.31$, $df = 16$, $p < 0.001$; Appendix C, Fig. S3-5). Stronger shifts towards nocturnal activity were also more likely to be detected via direct observation of lions ($F = 9.49$, $df = 2$, $p = 0.002$; Appendix C, Fig. S3-4). However, this pattern was largely driven by a single study that observed the largest difference in lion nocturnality between low vs. high disturbance areas, and which was one of the few studies that relied on direct observation as opposed to GPS collars or camera traps. The exclusion of this outlier (Dixon test, *Q* = 0.454, *p* = 0.02) eliminated the statistical significance of these effects (median date: *F* = 0.145, *df* = 15, *p*= 0.709; observation type: *F* = 2.59, *df* = 2, *p* = 0.11), and so this result is considered unreliable and disregarded for the remainder of the study.

Table 3-1: Top-performing mixed-effects models (within 2 ΔAICc from the lowest AIC_c model) and global models, with model evaluation parameters, used to assess the effects of ecological and anthropogenic local conditions on the magnitude of lion responses (SMD and RR) to human disturbance. SMD_w = average weighted standardized mean difference (REM intercept); RR_w = average weighted log response ratio (REM intercept); HFI_{sp} = spatial variation in human footprint index; CAT_a = average cattle production; $NDVI_{sp}$ = average spatial variation in NDVI; $NDVI_{tm}$ = temporal variation in NDVI; $NDVI_a$ = average overall NDVI.

Mixed-effects models	**AIC_c**	**ΔAIC_c**	**Model weight**	**$\hat{\tau}^2$ 95% CI**	**I^2 95% CI**	**Average ES (95% CI)**
Spatial responses						**SMD_w**
$HFI_{sp} + NDVI_{sp} + NDVI_{tm}$	52.95	0	0.45	0.108-0.449	82.2-95.0%	-0.268 (-0.433, -0.103)*
$HFI_{sp} + CAT_a + NDVI_{sp} + NDVI_{tm}$	53.34	0.38	0.37	0.099-0.432	80.6-94.8%	-0.279 (-0.437, -0.121)*
$HFI_{sp} + NDVI_{sp}$	54.79	1.83	0.18	0.132-0.491	85.0-95.5%	-0.254 (-0.437, -0.071)*
Global model	59.58	6.63		0.105-0.474	80.3-94.9%	-0.267 (-0.431, -0.103)*
Temporal responses						**RR_w**
$HFI_{sp} + CAT_a + NDVI_a + NDVI_{sp}$	-6.29	0	0.32	0.007-0.251	66.7-98.7%	-0.068 (-0.104, -0.033)*
$HFI_{sp} + CAT_a + NDVI_{sp}$	-6.12	0.17	0.29	0.005-0.219	73.1-99.1&	-0.075 (-0.115, -0.036)*
CAT_a	-5.42	0.87	0.20	0.006-0.183	81.7-99.3%	-0.089 (-0.142, -0.036)*
$CAT_a + NDVI_{sp}$	-5.27	1.02	0.19	0.005-0.189	76.4-99.2%	-0.070 (-0.119, -0.021)*
Global model	5.84	12.13		0.006-0.293	61.2-98.7%	-0.026 (-0.066, 0.013)

*coefficient 95% CI significantly different from 0

Discussion

At over two-thirds of the study sites, lions constrained their spatiotemporal niche to avoid humans by reducing their use of high human disturbance areas or limiting their daytime and crepuscular activity (Fig. 3-2a). The prevalence of these risk-averse behaviors highlights the tremendous scale of human effects on lions across a wide range of anthropogenic and ecological conditions, including in intensively managed reserves, and aligns with known patterns of human impacts on the spatiotemporal activity of mammals (Gaynor *et al.* 2018; Tucker *et al.* 2018). However, synthesizing lion responses across their range revealed that avoidance of humans is not uniform across lion populations. At almost one-quarter of the study sites, lions selected high-disturbance areas more often than low-disturbance areas. Our results indicate that lions are less likely to avoid human disturbance at sites with limited resource availability or fragmented habitats, possibly because resource limitation necessitates the expansion of their spatiotemporal niche (Fig. 3-3d,e). We also found that lions displayed stronger avoidance responses at sites where intensive cattle production could increase the risks of human-lion conflict (Fig. 3-3c). Overall, expanding human impacts and environmental changes across the range of lions threaten to downgrade their trophic impacts and are likely to intensify conflict with humans that is a primary threat to lion persistence (Hulme *et al.* 2001; Dixon *et al.* 2003).

Lions at sites with lower average NDVI or higher seasonal variation in NDVI – signaling limited or inconsistent primary productivity – were less likely to avoid human disturbance (Fig. 3-3d,e). Similarly, we found that increased variation in the human footprint, which could indicate fragmented suitable habitats and resources, contributed to diminished human-avoidance behaviors (Fig. 3-3a). Highly productive ecosystems that could support abundant wild prey populations, in contrast, led to spatiotemporal avoidance of human settlements by lions (Pettorelli *et al.* 2009; Fløjgaard *et al.* 2021). Where resources are scarce or heterogeneously distributed, lions have expanded their home ranges to meet their resource needs (Celesia *et al.* 2010; Tuqa *et al.* 2014). Climate changes across Africa are projected to exacerbate resource stress for humans and wildlife alike (Hulme *et al.* 2001; Thuiller *et al.* 2006; Intergovernmental Panel on Climate Change 2014; Wu *et al.* 2021), yet the effects of climate change are not usually emphasized in lion and other large carnivore conservation and threat assessments (Bauer et al., 2015; Di Minin et al., 2021; Lindsey et al., 2017; but see Carter et al., 2018). Our results indicate that niche expansion in response to spatial and temporal resource scarcity is consistent across lion populations and suggest the risks incurred by lions when encroaching on human-dominated areas can be outweighed by their metabolic needs. Additionally, the responses of lions to resource redistribution and degradation due to climate change and expanding anthropogenic land uses will likely expand the human-lion interface and amplify conflict, a result that highlights the synergy among various threats facing lion populations across their range (Bauer *et al.* 2020; Abrahms 2021). Our findings expand upon previous calls to dedicate adequate funding and management capacity to protected areas harboring lions (Packer *et al.* 2013; Lindsey *et al.* 2017), while engaging with and empowering local communities to invest in conservation initiatives (Constantino *et al.* 2012; Milupi *et al.* 2020). In particular, we emphasize the need to protect areas that are projected to be refugia from both climate risks and human expansion, as well as corridors that connect suitable lion habitats (Cushman *et al.* 2018; Loveridge *et al.* 2022).

Highly varied NDVI across a landscape, which could signal increased habitat structure that can diversify the available niches for herbivore prey species (e.g., habitat for both browsers and grazers), produced stronger human-avoidance behavior on both the spatial and temporal axes (Fig. 3-3b). Habitat structure can also provide optimal hunting grounds for lions (Du Toit & Cumming 1999; Cromsigt *et al.* 2009). Thus, spatial variation in primary resources could improve habitat quality for lions and their prey. Management that encourages diverse habitat structures in protected areas, such as preventing woody encroachment in savannas to maintain intermediate levels of woody cover, could benefit lion populations by supporting more diverse and abundant assemblages of wild prey (Schmitt *et al.* 2022). Heterogeneous NDVI patterns could alternatively be interpreted as less reliable forage resources to support prey species (Borowik *et al.* 2013). However, our other model results indicate that less reliable resource availability leads to more risk-taking behaviors by lions, and thus the observed increase in human avoidance given more heterogeneous NDVI does not support this interpretation (Fig. 3-3d,e).

At sites with higher cattle production, we found that lions increased their nocturnal behavior in response to human disturbance (Fig. 3-3c). The shift of lions to more nocturnal activity might signal that lions are targeting livestock as prey at these sites because lions are specialized for nighttime hunting and doing so diminishes the risks of encountering humans. Livestock depredation is a primary driver of conflict between lions and humans, which can result in retaliatory killing of lions and threatens lion population growth as well as food and economic security for human communities (Carter & Linnell 2016; Bauer *et al.* 2020; Di Minin *et al.* 2021). Alternatively, avoiding humans at these sites may suggest that high-intensity cattle production is exacerbating the disturbances caused by human activities or could reflect prevalent commercial farming that is more likely to exclude predators with fencing and other infrastructure. Though lions are primarily nocturnal, they commonly exploit hunting opportunities during crepuscular and daytime periods and may be forfeiting access to important resources by constricting their temporal niche in response to humans (Cozzi *et al.* 2012; Dröge *et al.* 2017). Livestock production can degrade habitats for the wild ungulates that lions prefer as prey items (Valeix *et al.* 2012; Davidson *et al.* 2013) by monopolizing grazing resources and waterholes as well as amplifying the spread of diseases (Carter *et al.* 2018; Easter *et al.* 2018). Where humans accompany grazing livestock herds across large swaths of the landscape during the day, the risks of human encounters and displacement of wild prey from grazing areas may cause lions to avoid activity during daytime hours. Whether lions perceive livestock to be a prey resource or a habitat disturbance, collective action within pastoralist communities is likely among the most important steps toward ameliorating negative lion-human interactions. Residents can simultaneously protect their livelihoods and improve lion habitats and survival through proactive husbandry practices (Ogada *et al.* 2003) and community-based conservation efforts that create co-benefits for people and wildlife (Blackburn *et al.* 2016; Killion *et al.* 2021).

Notably, we did not find evidence to suggest that lions in fenced reserves are less responsive to disturbance (Appendix C, Fig. S3-4). Many intensively managed fenced reserves, particularly in South Africa, house relatively high-density lion populations that could be shaped by intraspecific interactions to a greater extent than free-roaming populations (Packer *et al.* 2013). Fences create a distinct separation of wildlife from human impacts and should reduce the direct risks posed by humans, which could reasonably lead to higher use of areas near reserve edges and a broader spatiotemporal niche. However, our analyses indicate similar responses to human disturbance by lions in fenced and unfenced reserves, suggesting that the reduction of risk from human disturbance does not necessarily lead to diminished avoidance of humans by lions. Our results may indicate that environmental conditions that govern resource availability in space and time are more important in driving lion spatiotemporal behaviors than the risks posed by human disturbance itself.

Our results demonstrate that human disturbances constrain the realized spatiotemporal niche of lions throughout much of their range. Expanding habitat degradation due to human activities and climatic variability also threatens the capacity of lions to avoid humans and the risks associated with them. As wildlife monitoring efforts continue to expand, future work can build on these findings by explicitly incorporating local-scale interactions that were beyond the scope of this analysis. For example, inter- and intraspecific effects within large carnivore communities could cause lion population declines when disturbance favors generalist competitors (Green *et al.* 2018), or lead to more risk-taking behaviors when subordinate individuals are pushed into lower-quality, high-disturbance habitats. Site-specific estimates of wild prey availability could similarly improve our ability to explain lion responses to human disturbance, as the link between primary productivity and wild prey populations can be decoupled by management strategies or poaching pressures (Hayward *et al.* 2007; Craigie *et al.* 2010). There may also be interactions among anthropogenic and environmental conditions at the site level, such as the transition of livestock from a disturbance that reduces habitat quality to an attractive resource for lions when primary productivity (and by extension, the availability of wild prey) declines.

Expanding human impacts will reduce suitable habitat and resource availability for wildlife worldwide, and our results indicate that predators will increasingly access more disturbed areas to acquire adequate resources, possibly including targeting livestock as prey items. Human-carnivore conflict is already a primary cause of predator declines worldwide, and our results suggest that the interface between predators and humans will increase in coming years and potentially exacerbate large carnivore population declines (Treves & Karanth 2003; van Eeden *et al.* 2018). Large carnivores and other wildlife usually seek to avoid overlap with humans in space and time (Gaynor *et al.* 2018; Tucker *et al.* 2018; Ripari *et al.* 2022), but their ability to do so likely depends on access to relatively stable and predictable environments. Where avoidance of humans is infeasible, carnivores likely face increased risks from human-caused mortality and inadequate habitat quality to support viable populations (Ripple *et al.* 2014). In the face of human-driven global change that will intensify environmental variability, successful large carnivore conservation and sustainable coexistence with humans could hinge on the protection and connection of resource-rich habitats and refugia from human disturbances.

Acknowledgments

The lion monitoring data used in this study are the product of massive fieldwork and organizational efforts from numerous research groups, field teams, and study systems across the contemporary range of lions. We thank all of the research teams and contributors of each of the studies used here for their efforts and for transparent data reporting that enabled their inclusion in our meta-analysis. We also thank I. Sankaran for help with the preliminary literature review.

Chapter IV

Primary Resource Availability Underpins Human-Carnivore Conflict in Northern Botswana

Preamble: This chapter is in preparation for submission to the journal *Conservation Biology.* The citation for this chapter is: Mills, Kirby L., E. Bennitt, K. Zhu, H. Bartlam-Brooks, T. Hubel, A. Wilson, N. H. Carter, and N. J. Sanders. Primary resource availability underpins human-carnivore conflict in northern Botswana. *In prep*.

Abstract

Livestock depredation by large carnivores is among the foremost threats to carnivore conservation and severely impacts human well-being worldwide. While climate change presents additional multifaceted threats to wildlife and humans, the synergistic pathways through which novel environmental conditions can amplify human-wildlife conflict are largely unexplored. We assessed how environmental heterogeneity interacts with wildlife distributions to influence human-carnivore conflict, using insights from ecological theory to test whether bottom-up resource availability shapes wild prey availability and large carnivore selection for livestock prey (i.e., via prey switching or apparent competition). Specifically, we used zero-inflated Poisson mixed-effect models and binomial logistic regression to combine remotely sensed estimates of primary resources (i.e., water availability and primary productivity), wild prey movement, and seven years of reports for livestock depredation by African lions (*Panthera leo*) in the

Makgadikgadi Pans ecosystem, Botswana. Though we observed no trends in livestock depredation between wet vs. dry season periods, analyses at finer temporal scales revealed higher incidences of livestock depredation at times of primary resource scarcity including reduced primary production and water availability. We found no direct link between wild prey availability and livestock depredation rates, despite prey availability being strongly driven by primary productivity. Instead, our results suggest that livestock depredation may be more strongly influenced by livestock and lion responses to resource availabilities, a process largely overlooked in most human-carnivore conflict studies. Our findings provide insight into tailoring potential conflict mitigation strategies to fine scale changes in resource conditions to efficiently reduce conflict and support human livelihoods.

Introduction

Conflict between humans and large carnivores due to livestock depredation is a major threat to both large carnivore conservation and human livelihoods (Treves & Karanth 2003; Braczkowski *et al.* 2023). Human-carnivore conflicts are expected to intensify as climate change redistributes resources and wildlife in space and time (Fuller *et al.* 2016; Tucker *et al.* 2018; Guiden *et al.* 2019; Abrahms *et al.* 2023). In particular, patterns in herbivore abundances can be interrupted by human-caused environmental changes such as reductions in forage quality or drought, or artificial waterpoints (Smit *et al.* 2007; Harris *et al.* 2009; Middleton *et al.* 2013; Goswami *et al.* 2021). Though fluctuations in prey availability are linked to livestock depredation rates (Valeix *et al.* 2012; Amador-Alcalá *et al.* 2013; Kabir *et al.* 2014), the pathways through which bottom-up changes in primary resources and prey availability may escalate livestock depredation and threaten vulnerable human livelihoods are largely unexplored.

Here, we examine the relationships among resource availability, wild prey distributions, and livestock depredation by African lions (*Panthera leo*). Though they are an iconic species of conservation concern, lions are conflict-prone throughout their range and cause severe economic impacts for local communities (Di Minin *et al.* 2021; Braczkowski *et al.* 2023). Several studies have highlighted seasonal trends in livestock depredation by lions; however, understanding why there is seasonal variation, especially in the context of ecological theory, can enable more targeted and efficient conflict mitigation efforts (Miller & Schmitz 2019; Wilkinson *et al.* 2020).

The environmental drivers of lion predation on livestock are mediated by heterogeneity in the relationships among predators, prey, livestock, and primary resources. Livestock depredation by lions might increase in dry seasons, presumably when wild prey availability is limiting, leading lions to switch from wild to domestic animals (Schiess-meier 2007; McNutt *et al.* 2017).

Alternatively, higher precipitation can lead lions to switch their prey selection to livestock, possibly because wild prey are dispersed more widely across a resource-rich landscape and are thus less accessible (Patterson *et al.* 2004; Sogbohossou *et al.* 2011; Olivier *et al.* 2022). A final possibility is that apparent competition may intensify livestock depredation when abundant wild prey support high densities of lions but become more inaccessible than livestock through effective predator-avoidance (Hatton *et al.* 2015; Riginos 2015; Beattie *et al.* 2020).

To examine how bottom-up resources shape wild prey availability and rates of livestock depredation by large carnivores, we combined remotely sensed estimates of dynamic water availability and vegetation greenness (a common proxy for primary productivity), hourly wild prey telemetry locations, and seven years of incident reports for livestock depredation by African lions in northern Botswana. Specifically, we test whether (1) higher water availability and greenness increases prey availability and decreases rates of livestock predation reports; and (2) abundant prey reduces the incidence of livestock depredation by lions via prey switching or intensifies depredation via apparent competition. Our results can inform management practices in complex social-ecological systems and indicate that changes in climate-driven resource availability may have unforeseen consequences for human-carnivore conflict in communities worldwide.

Methods

Study area

The focal study area is approximately 5,000-km^2 in northern Botswana (24.9-25.5°E, 20.0-20.7°S) between the village of Gweta, the eastern boundary of the Makgadikgadi Pans National Park (MPNP), and the Ntwetwe salt pan (Fig. 4-2). There are two broad categories of vegetation in the study area (Brooks 2005): pan grassland closer to the salt pans (primarily *Cenchrus ciliaris* and *Sporobolus ioclados*) and mixed woodland elsewhere (primarily *Colophospermum mopane* and *Combretum imberbe* trees with *S. ioclados* grasses). The study area is composed of lands designated for photographic tourism (primarily CT11 in Fig. 4-1) and livestock grazing (primarily in CT7 and NG51 in Fig. 4-1). Livestock herds are housed at clusters of individual farms, locally referred to as cattle-posts. Livestock are unpenned to graze unattended during the day, returning to the cattle-posts in the evening for water and protection though some animals (up to 13% of individuals) may not return to the cattle-posts at night when they are most vulnerable to predators (Hemson *et al.* 2009).

The dominant wildlife in this system are plains zebra (*Equus quagga*) and blue wildebeest (*Connochaetes taurinus*), with herds numbering up to 24,000 and 10,000 individuals, respectively

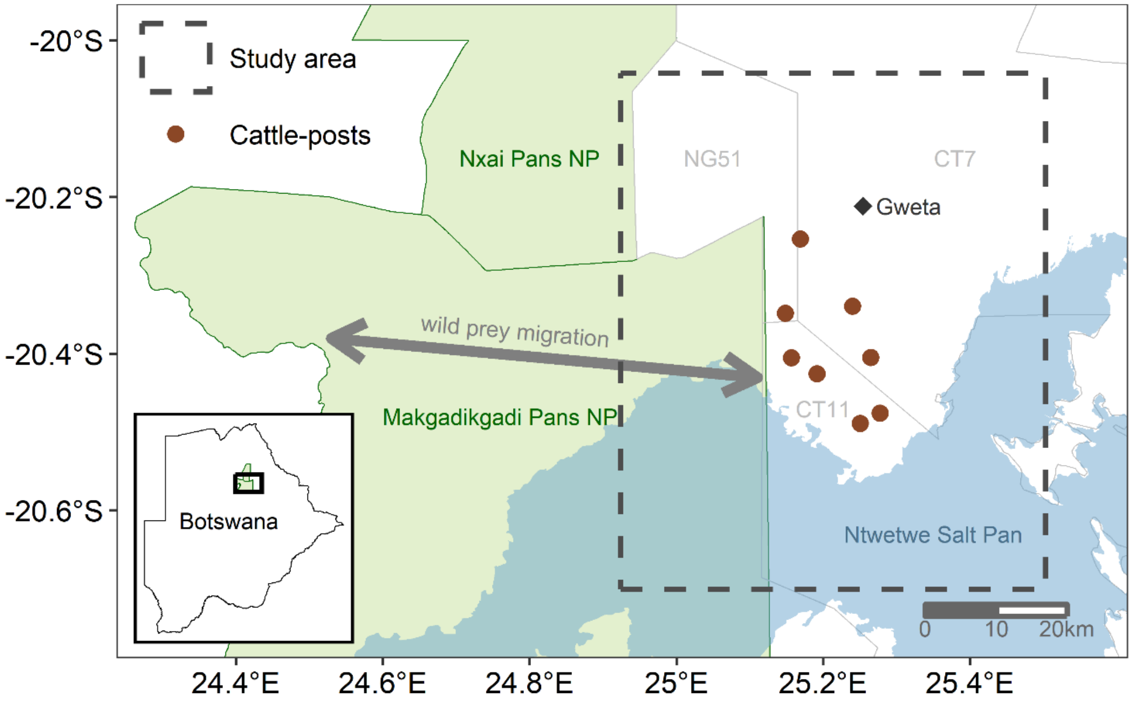

Figure 4-1: Study area location with respect to the Makgadikgadi and Nxai Pans National Parks (NPs) in northern Botswana. Circle points represent the locations of the 8 cattle-posts included in the study. The gray arrow spanning the NPs depicts the general path of the seasonal migration of wild prey (i.e., zebra and wildebeest) from their eastern wet season range to their western dry season range.

(Chase *et al.* 2015). Both species migrate *en masse* across the approximately 6,000-km^2 MPNP between the wet and dry season. In the rainy season (~December-April), zebra and wildebeest herds usually reside near the southeastern Ntwetwe salt pans where they forage and have access to water. When foraging opportunities and water dwindle in the dry season (~May-November), the ungulates migrate to the Boteti River on the western MPNP border that generally provides potable water year-round (Loveridge *et al.* 2010). However, changes in water availability interrupt the timing of this seasonal migration (Bennitt *et al.* 2022). This migration of wild prey has been suggested to impact rates of livestock depredation at the seasonal scale, because lions preferentially prey on wildebeest and zebra but may increase selection for livestock prey when wild prey migrate away from lion home ranges (Hemson 2003; Valeix *et al.* 2012). Other large ungulate species are present year-round in the study area (such as greater kudu [*Tragelaphus strepsiceros*], gemsbok [*Oryx gazella*], and hartebeest [*Alcelaphus buselaphus*]), but at lower densities relative to zebra and wildebeest. Though not censused in recent years, lions are reported to be the most abundant large carnivore in the study area by local tourism operators and residents, though leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), spotted hyena (*Crocuta crocuta*), and brown hyena (*Hyaena brunnea*) are also present (DEA 2010; Ngaka 2015).

Livestock depredation

To measure rates of livestock depredation by lions in the study area, we used Problem Animal Control (PAC) data which are collected and maintained by Botswana's Department of Wildlife and National Parks (DWNP). PAC data are the basis for Botswana's national compensation program that reimburses residents for losses to wildlife to incentivize conservation efforts and reduce retaliatory killings of animals. Because residents receive no compensation for livestock losses to unprotected predators, such as spotted hyenas, or lower compensation rates to others, such as leopards and wild dogs, there is some potential for bias in the PAC data if livestock killings are falsely attributed to lions (LeFlore *et al.* 2019). However, because other large predators in our study area are relatively rare and have generalist diets with low dietary overlap with lions (Hayward 2006; Hayward & Kerley 2008), we expect the occurrence of this error to be low and not associated with our explanatory variables of interest.

We received digitized PAC data from January 2015-December 2021, courtesy of DWNP. Because the PAC data include only the names of cattle-posts and do not include the exact locations of livestock depredation events, we assigned the location of the reports to the geographic centroid of the cluster of farms making up each cattle-post. Individual cattle-post farms were identified and geolocated during fieldwork in the study area in June-July 2022. We filtered the PAC data to cattle-posts that are < 20-km from MPNP and with > 10 total PAC reports during the study period. In doing so, we included the 8 cattle-posts that were most likely to be influenced by patterns in wild prey and seasonal resource availability while limiting analytical complications due to zero-inflation (Fig. 4-1). We summed the total number of PAC reports for every month from January 2015-December 2021 to create two data sets for subsequent modeling: 1) monthly PAC reports for all cattle-posts together (i.e., PAC total per month, $N = 84$) and 2) monthly PAC reports for individual cattle-posts (i.e., PAC total per month x 8 cattle-posts, $N = 672$).

Wild prey availability

Between 2016-2018, 10 zebra and 18 wildebeest from independent social groups were fitted with GPS collars to track herd movements across MPNP (Bennitt *et al.* 2022). All collaring methods and data collection were conducted under research permits from the Ministry of Environment, Natural Resources Conservation and Tourism (EWT 3/3/8 XXXVIII, EWT 8/36/4 XXIV (199)) and were approved by the Ethics and Welfare Committee of the Royal Veterinary

College (RVC 2013 1233). GPS collars were custom-built by the Royal Veterinary College and designed to collect fixes every 5-minutes with pre-programmed drop-off mechanisms to be activated after 18-months of deployment (Wilson *et al.* 2013; Curtin *et al.* 2018). We used the prey GPS locations, resampled to 1-hour intervals, to assess relative prey abundance by calculating the proportion of collared individuals present in the study area for each month between May 2016-December 2018 ($N = 32$).

Environmental data

We assessed three environmental variables that are often correlated with resource availability in arid ecosystems: 1) precipitation, 2) surface water availability, and 3) primary productivity.

Monthly precipitation data were extracted from the CHELSA global climatologies dataset averaged across the entire spatial extent of the study area (Karger *et al.* 2017b, a). CHELSA precipitation data are available only until June 2019, and so further analyses including precipitation variables are all truncated to that period (i.e., excluding PAC data from July 2019-December 2021). We calculated the lagged precipitation for each month by averaging the amount of precipitation in the current and preceding two months, which we viewed as a compromise between detecting the immediate effects of precipitation to provide drinking water for animals and longer-term effects on vegetation growth (Olivier *et al.* 2022).

Surface water availability within the salt pans was assessed by calculating the Normalized Difference Water Index (NDWI) that uses a ratio of green and infrared bands (GREEN - NIR/ GREEN + NIR) to delineate open water features (McFeeters 1996; Ji *et al.* 2009). Generally, positive NDWI values correspond to water surface and negative values represent non-aqueous surfaces. The NDWI values were derived using the USGS Landsat 8 satellite imagery (30-km resolution) at a 16-day temporal resolution. We removed the clouds from the satellite images, calculated the NDWI for each pixel in the image set, and created a mosaic of the average pixel value for each month. We then calculated the average monthly NDWI value within the intersection of the salt pan boundaries and the study area to represent the relative amount of water available to wildlife.

To estimate primary productivity and thus the forage quantity for wild herbivores and livestock, we used the Normalized Difference Vegetation Index (NDVI) time series dataset at 8-day resolution provided by MODIS Land Products data (250-m resolution). NDVI data were averaged within a circular buffer around each cattle-post for each month. We tested the sensitivity of our extraction of NDVI at three buffer sizes: 3-km, 5-km, and 10-km radii, but found that all three buffer distances provided similar results. We thus chose to use the average NDVI within 10-km of the cattle-posts to provide the most comprehensive measure of foraging available to livestock. Because wild prey are not tied to cattle-post locations, we also calculated the average NDVI across the entire spatial extent of the study area.

Statistical analyses

To assess overall trends in livestock depredation, we tested for differences in the average monthly PAC reports between the peak wet season (Dec.-Feb.) and the peak dry season (Jun.-Aug.) using a Mann-Whitney *U* test. We also tested for differences in monthly reports among years with a Kruskal-Wallis test. Non-parametric tests were used because monthly PAC data were not normally distributed among groups.

We used a logistic regression model to test the effects of bottom-up resource availability on monthly prey abundance in the study area, using the binomial family with the response variable constructed as the number of "successes" (collared prey present in the study area) and "failures" (collared prey absent) (Douma & Weedon 2019). We similarly modeled the number of monthly

PAC reports at each cattle-post in response to resource availability with a zero-inflated Poisson mixed effects model, which is most appropriate for count data such as those analyzed here, using R package ‘GLMMadaptive’. We included zero-inflation to account for many months with zero PAC reports when separated by cattle-post, and we accounted for inherent variation in cattle-posts by including cattle-post ID as a random effect. In both models, we compared all combinations of a global model including the three environmental variables as predictors: average NDVI (across the study area for prey availability, or surrounding cattle-posts for depredation reports), average NDWI of the salt pans, and lagged precipitation (3-month average of total precipitation). All environmental variables were scaled and centered to produce comparable model coefficients. Finally, to compare the relative effects of prey and resource availabilities, we used a Poisson regression to test the effects of wild prey abundance and all three environmental variables on the total number of livestock depredation reports (aggregating all cattle-posts) for months with prey

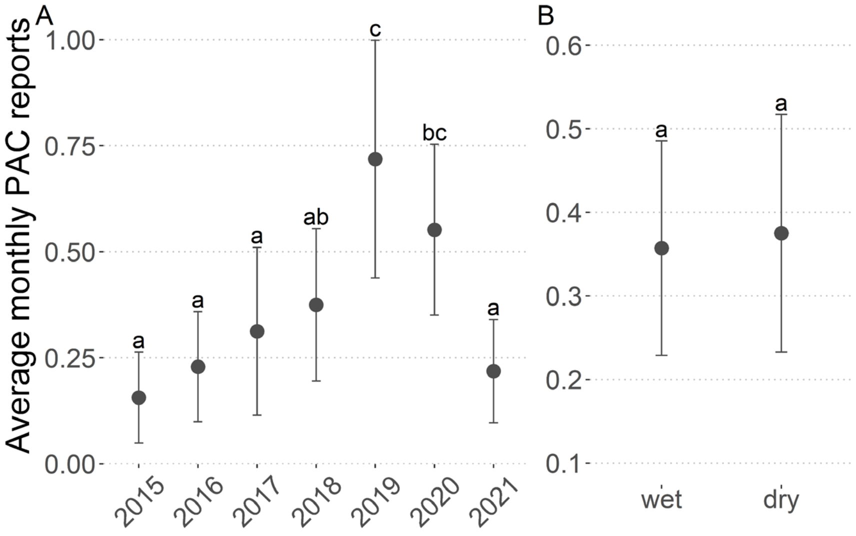

Figure 4-2: Differences in monthly livestock depredation reports (A) among years and (B) between peak wet vs. dry seasons. Letters indicate significant differences among groups according to (A) Kruskal-Wallis tests or (B) Mann-Whitney U, respectively. Error bars represent 95% CIs.

availability data (N = 32). This model did not include zero-inflation because there was a low proportion of months with zero PAC reports when in the cattle-post aggregated dataset.

Because the lagged precipitation and average NDVI were highly correlated ($r > |0.6|$), we excluded models with both variables during model evaluation. We compared models for monthly PAC reports using the Akaike Information Criterion (AIC) and models of total PAC reports and monthly prey availability using AIC corrected for small sample sizes (AIC_c). We considered models to be similar in performance if they did not differ by > 2 $\Delta AIC/AIC_c$ (Burnham *et al.* 2011). If the lagged precipitation variable was not included in the best performing model for PAC reports, we removed this variable from the global model and then re-compared the global model combinations using the full dataset of depredation reports.

Results

From 2015 to 2021, a total of 246 livestock depredation reports were attributed to lions in the study area. Monthly reports of depredation by lions generally increased over time with the highest levels of depredation reported in 2019 and 2020 (Kruskal-Wallis $\chi 2 = 31.64$, df = 6, p <

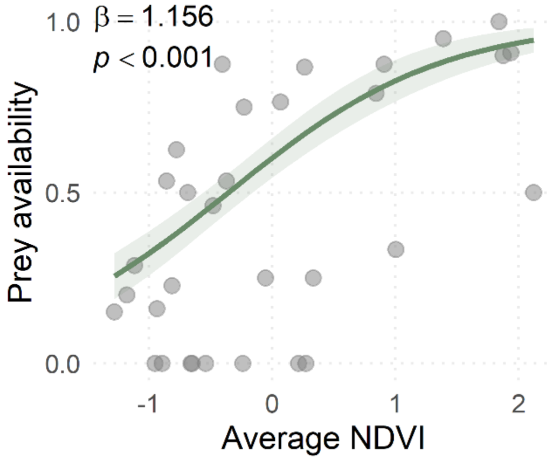

Figure 4-3: Fitted effects of average NDVI in the study area on monthly prey availability. Fitted relationship (with 95% confident intervals) and statistics (β coefficient and associated *p*-value) represent logistic regression model results. Prey availability is measured as the proportion of collared prey individuals present in the study area per month.

0.001), though there was a notable decline in reports in 2021 (Fig. 4-2A). We found no differences in the number of livestock depredation reports between the wet and dry seasons (Wilcoxon W = 14.247, p = 0.83; Fig. 4-2B). The best logistic regression model showed that relative prey abundance in the study area increased as NDVI increased (β = 1.16, 95%CI: 0.89, 1.45; p < 0.001; Fig. 4-3, Table 4-1), with each 0.1 increase in unscaled NDVI resulting in a 16% increase in prey availability.

The number of livestock predation reports was best predicted by the combination of water availability and primary production (Table 4-1). Zero-inflated Poisson mixed effects modeling indicated that livestock depredation reports were highest during months with low salt pan NDWI (β = -0.255, 95%CI: -0.46, -0.05; *p* = 0.01) and low average NDVI in the study area (β = -0.148, 95%CI: -0.34, 0.04; *p* = 0.13; Fig. 4-4), though the latter was not a significant effect. In other words, a 0.1 increase in unscaled salt pan NDWI or study area NDVI reduces the expected count of PAC reports by 7.1 % and 1.4%, respectively. The monthly availability of wild prey, however, was less informative than environmental predictors of the total number of livestock depredation

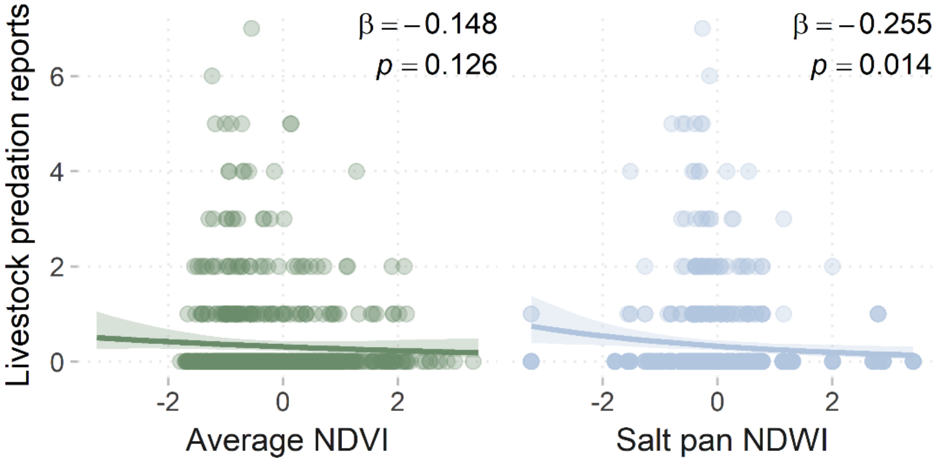

Figure 4-4: The effects of primary resource availability on the monthly number of livestock depredation reports attributed to lions. Fitted relationships (with 95% CIs) and statistics (β coefficients and associated *p*-values) represent results of the top-performing zero-inflated Poisson mixed-effects model, including cattle-post ID as a random effect. Average NDVI: the monthly average of NDVI within 10-km of a cattle-post. Salt pan NDWI: monthly average of NDWI within the salt pan and study area boundaries.

reports across the study area. The top-performing Poisson regression model showed that PAC reports increased when NDWI was lowest ($\beta = -0.220$, 95%CI: -0.42, -0.03; $p = 0.03$) and when precipitation was highest ($\beta = 0.235$, 95%CI: 0.06, 0.40; $p < 0.01$; Table 4-1). The next highest-performing model ($\Delta\text{AIC}_c = 1.3$) included prey abundance as a predictor of total PAC reports but showed an insignificant effect ($\beta = -0.128$, 95%CI: -0.35, 0.09; $p = 0.26$).

Table 4-1: Statistical models within <2 $\Delta\text{AIC}/\text{AIC}_c$ of the top-performing model evaluating the effects of bottom-up resource availability on monthly prey abundance and livestock depredation, including scaled model coefficients (with 95% CIs).

		Model coefficients (95% CI)					
		Average NDVI	**Average salt pan NDWI**	**Lagged precipitation**	**Prey abundance**	**Model comparison**	
Prey abundance models		*Study area*				AIC_c	ΔAIC_c
Binomial logistic	*NDVI*	1.156* (0.89, 1.45)	-	-	-	145.6	0
	NDVI + NDWI	1.147* (0.87, 1.44)	0.039 (-0.18, 0.26)	-	-	147.5	1.9
Total PAC reports models						AIC_c	ΔAIC_c
Poisson	*NDWI + Precip*	-	-0.220* (-0.42, -0.03)	0.235* (0.06, 0.40)	-	197.6	0
	NDWI + Precip + Prey	-	-0.215* (-0.43, -0.01)	0.292* (0.09, 0.48)	-0.128 (-0.35, 0.09)	198.9	1.3
Cattle-post PAC reports models		*Cattle-post*				AIC‡	ΔAIC‡
Zero-inflated Poisson†	*NDVI + NDWI*	-0.148 (-0.34, 0.04)	-0.255* (-0.46, -0.05)	-	-	1019.3 (588.6)	0 (1.7)
	NDWI	-	-0.268* (-0.46, -0.07)	-	-	1019.7 (589.8)	0.4 (2.9)
	NDVI	-0.173^{+} (-0.36, 0.01)	-	-	-	1023.3 (586.9)	4.0 (0)

Coefficient significance: $^{*}p < 0.05$, $^{+}p < 0.1$

†Zero-inflated Poisson models include a random effect of cattle-post ID.

‡AIC and ΔAIC values in parentheses represent the AICs of models including only observations with precipitation data.

Average NDVI (Study area): monthly average of NDVI across the study area extent

Average NDVI (cattle-post): monthly average of NDVI within 10-km of a cattle-post

Salt pan NDWI: monthly average of NDWI within the salt pan and study area boundaries

Lagged precipitation: 3-month average of total monthly precipitation

Prey abundance: monthly proportion of collared prey individuals present in the study area

Discussion

Our results suggest that bottom-up resource availability is more important in shaping rates of livestock depredation than the availability of wild prey in the Makgadikgadi Pans ecosystem, despite a clear relationship between resource availability and prey abundances. We found that livestock depredation is most likely when water and forage resources are limited and likely cause wildlife and livestock to adjust their foraging behaviors. However, we did not detect a direct link between monthly prey availability and livestock depredation, indicating that neither prey switching by lions nor apparent competition between livestock and wild prey are prominent drivers of depredation events. Instead, we posit that the foraging ranges and activity of wild prey, livestock, and lions are fundamentally driven by primary resources in unique ways, shaping their vulnerability to predation. Given the predicted redistribution of primary resources in space and time due to ongoing climate change, particularly increasing drought prevalence and reduced primary productivity, our results echo recent projections of increasing human-carnivore conflict (Hulme *et al.* 2001; Wu *et al.* 2021; Abrahms *et al.* 2023).

Most studies investigating the effects of primary resources on livestock depredation do so only in the context of resource effects mediated through wild prey availability; the effects of resource availability on livestock ecology are generally overlooked (Patterson *et al.* 2004; Wilkinson *et al.* 2020; Olivier *et al.* 2022). Similar to wild prey, cattle distributions and movement can be strongly driven by the availability of forage and water resources particularly in semi-arid systems such as the Makgadikgadi Pans (Scoones 1995; Butt 2010; Feldt & Schlecht 2016). However, wild prey and livestock in our study area respond to limited resource availability in different ways. While wild prey can leave to seek out resources elsewhere (such as the other side of MPNP), livestock are tethered to their home cattle-posts and likely extend their ranging behaviors in search of foraging opportunities and water. Indeed, participatory mapping research on the west side of MPNP suggests that free-roaming cattle increase their home ranges during the dry season when resources are scarce (K. Orrick, *unpublished data*). Because livestock are not actively herded in the Makgadikgadi Pans, they forage without human-imposed restrictions and effectively serve as resident prey (as opposed to migratory prey) with a unique ecology. Our findings suggest that livestock serve as a prey resource for a generalist predator (i.e., lions) that increases kill rates on livestock not because wild prey is less available, but because livestock become more accessible and vulnerable to predation. This is in line with Miller & Schmitz's (2019) conceptualization of predator-prey interaction theory in the context of livestock depredation, but our findings extend this theoretical framework to consider depredation driven by habitat domain shifts in livestock in addition to predators and wild prey.

Reductions in resource availability due to climate change are also likely to cause more risk-taking behaviors in lions and other large carnivores, possibly resulting in higher incidences of human-carnivore conflict (Mills et al., *in review*; Tuqa et al. 2014). Increased livestock depredation rates may be reflective of larger lion home ranges and increased overlap with high-risk, human-dominated areas, incidentally leading to higher encounter rates with livestock. Importantly, the combination of lion, livestock, and wild prey responses to limited resource availabilities could be synergistically contributing to escalated livestock depredation. Future work that integrates wildlife and livestock movements in response to environmental heterogeneity at fine spatiotemporal scales could help further tease apart these complex relationships.

Our results run counter to previous works in MPNP that suggest clear-cut seasonal trends (e.g., wet vs. dry season) in livestock depredation rates (Valeix *et al.* 2012), indicating that environmental heterogeneity shapes conflict at finer temporal scales. As such, seasonal recommendations for conflict mitigation measures are likely to be ineffective compared to those tailored to recent environmental conditions. Although employing herdsman year-round or seasonally may not be financially feasible for cattle-owners, it could be beneficial at lower costs to adaptively herd livestock only in months of increased depredation risk. Residents around MPNP often look to governmental intervention as a solution to conflict, such as large-scale fencing to limit wildlife movement between MPNP and livestock grazing areas (Hemson *et al.* 2009). With guidance from our results, tourism operators and government agencies could tailor common ecosystem management strategies to mitigate conflict. For example, the provisioning of water resources via boreholes can influence herbivore distributions (Smit *et al.* 2007; Chamaillé-Jammes *et al.* 2016), though this could adversely impact other wildlife (Selebatso *et al.* 2018; Bennitt *et al.* 2022). Given lion selection for waterholes as hunting grounds (Valeix *et al.* 2010; Davidson *et al.* 2013), strategic placement of boreholes and timing of pumping could encourage spatial separation of lions and livestock at times of high conflict risk.

A common assumption is that prey availability is the primary driver of livestock depredation by large carnivores (Khorozyan *et al.* 2015), but our results do not support this assumption. Instead, we show that these patterns are underpinned by wildlife and livestock responses to fluctuations in primary resources. The presence of free-roaming cattle in sympatry with wildlife generates complex ecological interactions in which livestock, wild prey, and predators must all adaptively respond to changes in resource availability. As climate change limits resource availabilities worldwide, expanding home ranges and novel movement patterns of wildlife and livestock alike will likely lead to intensified human-carnivore conflict (Tucker *et al.* 2018; Abrahms *et al.* 2023). Our results highlight the synergistic threats of climate change amid growing concerns for the conservation of biodiversity and human wellbeing in coming years (Pecl *et al.* 2017; Martens *et al.* 2022). However, using insights from ecological theory to better understand human-wildlife conflict, one facet of climate change impacts, can help inform mitigation strategies for a dynamic and uncertain future.

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Chapter V

Conclusions

Summary

In this dissertation, I explored the multifaceted impacts of human disturbances and environmental change on wildlife communities. From direct human presence in **Chapter II** to fluctuating primary resources in **Chapter IV**, I demonstrated that large carnivores and their prey display complex responses to human disturbance that have critical implications for their ecological interactions and human-wildlife conflict. In **Chapter II**, I showed that direct human presence produces diverse behavioral responses in African large carnivores and herbivores that ultimately result in restructured overlap between predators and prey at the community level. With a focus on African lions, **Chapter III** demonstrates that even apex predators prefer to avoid human disturbance in space and time but are more likely to risk human encounters when resources are limited. Finally, I determined that human-lion conflict can be exacerbated by wildlife responses to declines in resource availability in **Chapter IV**, extrapolating from the results of previous chapters to highlight the complex community dynamics at play in systems where large carnivores, wild prey, and livestock co-occur. Altogether, this work demonstrates that humans can modify ecosystems in many complex ways that can synergistically modify wildlife activities and community dynamics.

Key takeaways & Implications

The risks posed by human disturbance, from direct human presence to the indirect infrastructural signal of human-dominated landscapes, generate a clear avoidance response in most wildlife species (Gaynor *et al.* 2018). I found that large carnivores and many of their wild prey species engage in risk-avoidance behaviors by reducing their overlap with humans both temporally (**Chapter II**) and spatially (**Chapter III**). Yet all animals are faced with the tradeoffs between avoiding risks while acquiring adequate resources for survival, as predicted by optimal foraging theory (Sih 1980; Brown *et al.* 1999). While **Chapters II** and **III** demonstrate that lions and their prey employ risk-avoidance (or antipredator) behaviors in response to humans, these responses are mediated by the availability of primary resources such as vegetation and water. As evidenced in **Chapter III**, the risks of encountering humans are outweighed by lions' metabolic needs when resources are scarce, leading to increases in spatial overlap and higher risks of conflict between lions and people. These results are corroborated by my findings in **Chapter IV** because limited resource availability was a primary predictor of elevated risks of livestock depredation by lions, likely because of a combination of lion, wild prey, and livestock responses to resource limitation.

A critical aspect of global climate change is the redistribution and reduction of primary resources, particularly across much of the African continent (Hulme *et al.* 2001; Wu *et al.* 2021). Given the wildlife responses to resource limitations observed here and similar findings elsewhere (Hetem *et al.* 2014; Tucker *et al.* 2018), we are likely to see increases in overlap and encounters between humans and wildlife. These impacts of climate change have recently been highlighted as an undervalued contributor to escalating human-wildlife conflict around the world (Abrahms *et al.* 2023). Importantly, areas where climate change is anticipated to affect resource availabilities often coincide with geographic regions where the socioeconomic burdens associated with climate change and human-wildlife conflict are felt most strongly (Dixon *et al.* 2003; Braczkowski *et al.*

2023). Though human-wildlife interactions have been studied extensively, achieving coexistence between people and wildlife in the face of climate change requires the integration of synergistic human and wildlife responses to climate change into a cohesive social-ecological framework (Lozano *et al.* 2019).

Whether humans modify interspecific wildlife interactions (**Chapter II**), induce antipredator responses (**Chapter III**), or provide additional prey resources for predators (**Chapter IV**), the addition of humans and their livestock on the landscape can add considerable novelty to the ecological interactions that govern ecosystems (Dorresteijn *et al.* 2015; Guiden *et al.* 2019). In the context of livestock depredation by carnivores, most research frames conflict as a byproduct of large carnivore behaviors and wild prey availability (e.g., Olivier et al., 2022; Patterson et al., 2004). Though we can use existing predator-prey theory to guide livestock husbandry practices in response to these processes (Miller & Schmitz 2019), it is equally important to better incorporate humans and livestock as active players in the ecological interactions that shape conflict (Wilkinson *et al.* 2020). **Chapter IV** highlights that the fluctuations in wild prey availability are not always the primary driver of livestock depredations, indicating that conflict is likely underpinned by the impacts of primary resource availabilities on lions and livestock as well. Particularly in our study system where livestock are not actively herded, a comprehensive understanding of the drivers of conflict requires incorporating livestock as a potential prey resource with unique ecological strategies into the context of the system.

Future directions

Fully integrating socio-ecological systems into theoretical frameworks requires multidisciplinary research that harnesses expertise and technologies from both the social and natural sciences. Despite the implications of human-wildlife conflict for peoples' well-being, the majority of conflict research studies – including the work in this dissertation - lack social data (Lozano *et al.* 2019; Braczkowski *et al.* 2023). There is also a dearth of research on the movements and behaviors of livestock in sympatry with wildlife. Camera trap studies provide a non-invasive method to sample wildlife, livestock, and human activities across a landscape (Burton *et al.* 2015; Harris *et al.* 2019), as demonstrated in Chapter II. However, this approach does not typically provide insights into the fine-scale interactions that take place as wildlife encounter humans and livestock or adaptively respond to changing environmental conditions. Similarly, single-species telemetry studies can assess wildlife responses to modified resource availabilities at fine spatiotemporal scales, such as the responses of wild prey to primary productivity illustrated in Chapter IV, but it is challenging to relate those data directly to interspecific interactions (i.e., between wild prey and predators or livestock). Community-scale telemetry data (i.e., simultaneously collecting GPS movement data from large carnivores, wild prey, and livestock) would provide a powerful tool to identify direct and indirect interspecific interactions and disentangle the complex responses of animals to each other and their environments. Finally, contextualizing the occurrence of observed livestock-predator interactions with the human experiences that accompany conflict is a key component in designing effective and efficient conflict mitigation strategies. The results of this dissertation provide foundational information that could guide the development of management techniques tailored to predictable and measurable environmental conditions. However, the effectiveness of such strategies hinges on further research into the fine-scale socioecological drivers of conflict and culturally specific human-wildlife interactions.

Appendices

Appendix A: Supplementary Tables and Figures for Chapter II

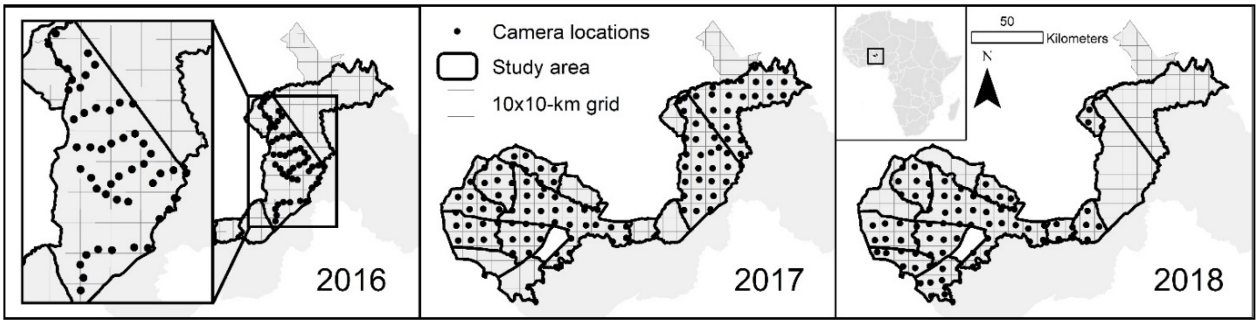

Figure S2-1: Camera placement in W-Arly-Pendjari protected area complex from three survey years. 50 cameras were deployed in 2016, 115 cameras in 2017, and 73 cameras in 2018. Modified from Mills et al. 2020.

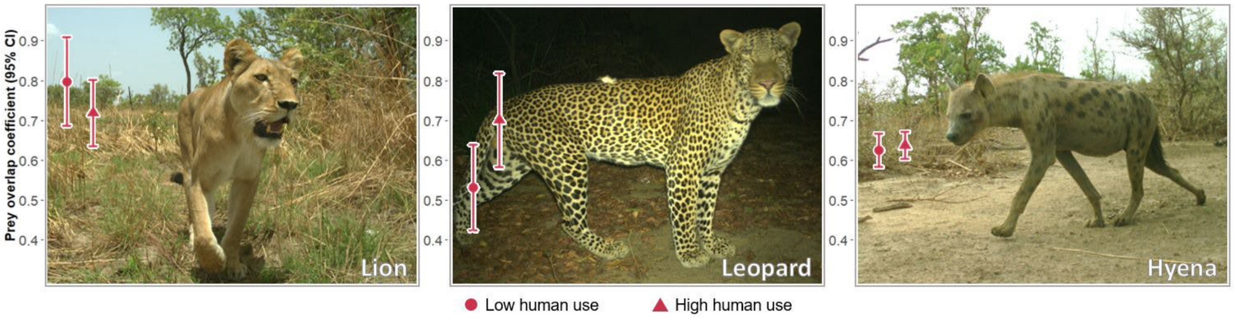

Figure S2-2: Temporal overlap coefficients (Δ) between each predator and their associated prey species. Buffalo not included as prey for African leopard. Error bars represent bias-corrected, bootstrapped 95% confidence intervals of coefficient estimates. Photo credit: Applied Wildlife Ecology Lab (AWE), University of Michigan, images from camera trap survey within the study area.

Table S2-1: Species detections (using 30-minute quiet periods) during the camera survey and common diel period. Asterisks (*) indicate significant shifts in diel activity distributions due to human presence. Changes in nocturnality are depicted for species with significant increases (+) and decreases (-) in response to humans. Empty cells represent no significant changes.

Species		Detections	Diel period[1]	Significant diel shift	Change in nocturnality
Apex Predators		**786**		*	
Hyena	*Crocuta crocuta*	628	crepuscular	*	
Leopard	*Panthera pardus*	62	nocturnal	*	
Lion	*Panthera leo*	96	nocturnal		
Ungulates		**10,325**		*	+
Buffalo	*Syncerus caffer brachyceros*	698	cathemeral		
Roan Antelope	*Hippotragus equinus koba*	990	diurnal	*	
Hartebeest	*Alcelaphus buselaphus major*	211	diurnal		
Waterbuck	*Kobus ellipsiprymnus defassa*	161	diurnal		
Bushbuck	*Tragelaphus sylvaticus*	2245	cathemeral	*	+
Kob	*Kobus kob kob*	847	diurnal	*	-
Reedbuck	*Redunca redunca*	1270	cathemeral	*	+
Aardvark	*Orycteropus afer*	261	nocturnal	*	-
Warthog	*Phacochoerus africanus*	1170	diurnal	*	+
Duiker	*Sylvicapra grimmia* *Cephalophus rufilatus*	1488	diurnal	*	+
Oribi	*Ourebia ourebi*	984	diurnal	*	

[1] Lamarque, F. (2004). *Les grands mammifères du complexe WAP*. CIRAD-ECOPAS, Montpellier.

Table S2-2: Human occupancy model selection table of top models with ΔAICc < 2 derived from camera data collected over 3 survey seasons in the W-Arly-Pendjari complex, West Africa. Detection (p) and occupancy (ψ) were modeled using the following covariates: CAM = camera type, SAV = percent savanna, YR = survey year, SITE = survey site, MGMT = management type (national park or hunting concession).

Candidate Models for Human Occupancy	AICc	ΔAICc	AICc weight	χ^2 Goodness-of-fit *p*-value	Occupancy Estimates	
					Mean	Var.
p (CAM + SAV + YR + SITE) ψ (YR)	826.73	0.00	0.47	0.327	0.543	0.160
p (CAM + SAV + YR + SITE + TN) ψ (YR)	828.67	1.94	0.18	0.363	0.545	0.160
p (CAM + SAV + YR + SITE) ψ (YR + MGMT)	828.70	1.97	0.18	0.359	0.540	0.166
p (SAV + YR + SITE) ψ (YR)	828.73	2.00	0.17	0.353	0.548	0.153

Table S2-3: Sensitivity analysis of species shifts in circular activity distributions, by adjusting the threshold value of human occupancy ± 0.1 from the mean. *P*-values are given for tests on species shifts using each threshold value. Sig. indicates the observed significance of shifts using the mean threshold value (0.54): + < 0.1, * < 0.05, ** < 0.01, *** < 0.001. The number of significant results (*p*-value < 0.05) using different threshold values is given, for which 3 indicates significance using all thresholds and 0 indicates no significance for any threshold.

Species	Human occupancy threshold			Sig.	# sig.
	0.44	0.54	0.64		
Apex predators	0.035	0.019	0.016	*	3
Hyena	0.012	0.014	0.005	*	3
Leopard	0.044	0.060	0.056	+	1
Lion	0.518	0.266	0.286		0
Ungulates	0	0	0	***	3
Aardvark	0.001	0.012	0.017	*	3
Buffalo	0.451	0.406	0.238		0
Bushbuck	0	0	0	***	3
Duiker	0.027	0.019	0.019	*	3
Hartebeest	0.363	0.229	0.233		0
Kob	0	0	0	***	3
Oribi	0	0	0.001	***	3
Reedbuck	0	0	0	***	3
Roan Antelope	0.026	0.076	0.107	+	1
Warthog	0	0	0.001	***	3
Waterbuck	0.053	0.118	0.098		0

Appendix B: Supplementary Methods and Results for Chapter III

Analysis for publication bias:

We assessed the presence of publication bias in the spatial and temporal lion response datasets with Egger regression tests of asymmetry for funnel plots that map effect size residuals against the corresponding sampling variances (Figure S3-5). While spatial lion responses showed symmetrical residuals ($z = 0.452$, $p = 0.652$), the regression test of temporal lion responses did suggest publication bias with significant asymmetry ($z = -4.12$, $p < 0.001$). However, tests for Rosenberg's fail-safe number revealed that the number of studies with null responses necessary to change the significance of our results was many times higher than the actual sample sizes of the models. To increase the observed significance of the mixed-effects models to > 0.05 would require including an additional 249 null spatial effect sizes and 191 null temporal effect sizes. The very large number of studies needed to nullify the observed significance of the mixed-effects models thus suggests that publication bias is unlikely to have substantially impacted our results. In addition, many studies included in this analysis were not explicitly designed to detect lion responses to human disturbance, which lessens the risk of publication biases that could compromise our results.

Spatial autocorrelation of effect sizes:

We tested the observed effect sizes of human disturbance on lion activity for spatial autocorrelation using Moran's *I* but found no significant autocorrelation for either spatial ($p = 0.20$) or temporal effect sizes ($p = 0.99$).

Study IDs and citations for data included in meta-analysis

1. M. Beukes, F. G. T. Radloff, S. M. Ferreira, Estimating lion's prey species profile in an arid environment. J. Zool. 303, 136–144 (2017).
2. R. Chaudhary, N. Zehra, A. Musavi, J. A. Khan, Evaluating the effect of ecological and anthropogenic variables on site use by sympatric large carnivores in Gir protected area, Gujarat, India. Wildlife Biol. 2020 (2020), doi:10.2981/wlb.00696.
3. S. Dolrenry, thesis (2013).
4. E. Dröge, S. Creel, M. S. Becker, A. J. Loveridge, L. L. Sousa, D. W. Macdonald, Assessing the performance of index calibration survey methods to monitor populations of wide-ranging low-density carnivores. Ecol. Evol. 10, 3276–3292 (2020).
5. E. Dröge, S. Creel, M. S. Becker, J. M'soka, Spatial and temporal avoidance of risk within a large carnivore guild. Ecol. Evol. 7, 189–199 (2017).
6. K. T. Everatt, J. F. Moore, G. I. H. Kerley, Africa's apex predator, the lion, is limited by interference and exploitative competition with humans. Glob. Ecol. Conserv. 20, e00758 (2019).
7. K. Gogoi, U. Kumar, K. Banerjee, Y. V. Jhala, Spatially explicit density and its determinants for Asiatic lions in the Gir forests. PLoS One. 15, 1–19 (2020).
8. D. S. Green, L. Johnson-Ulrich, H. E. Couraud, K. E. Holekamp, Anthropogenic disturbance induces opposing population trends in spotted hyenas and African lions. Biodivers. Conserv. 27, 871–889 (2018).
9. M. W. Hayward, G. J. Hayward, Activity patterns of reintroduced lion Panthera leo and spotted hyaena Crocuta crocuta in the Addo Elephant National Park, South Africa. Afr. J. Ecol. 45, 135–141 (2006).

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13. K. L. Mills, Y. Harissou, I. T. Gnoumou, Y. I. Abdel-Nasseer, B. Doamba, N. C. Harris, Comparable space use by lions between hunting concessions and national parks in West Africa. J. Appl. Ecol. 57, 975–984 (2020).
14. K. L. Mills, N. C. Harris, Humans disrupt access to prey for large African carnivores. Elife. 9, e60690 (2020).
15. N. L. Mogensen, J. O. Ogutu, T. Dabelsteen, N. L. Mogensen, J. O. Ogutu, T. Dabelsteen, N. L. Mogensen, J. O. Ogutu, T. Dabelsteen, The effects of pastoralism and protection on lion behaviour, demography and space use in the Mara Region of Kenya. African Zool. 46, 78–87 (2011).
16. A. Oriol-Cotterill, D. W. Macdonald, M. Valeix, S. Ekwanga, L. G. Frank, Spatiotemporal patterns of lion space use in a human-dominated landscape. Anim. Behav. 101, 27–39 (2015).
17. S. L. Schooler, S. P. Finnegan, N. L. Fowler, K. F. Kellner, A. L. Lutto, J. Parchizadeh, M. Van Den Bosch, A. Z. Perez, L. M. Masinde, S. B. Mwampeta, H. M. Boone, M. G. Gantchoff, J. E. Hill, T. M. Kautz, N. H. Wehr, R. Fyumagwa, J. L. Belant, Factors

influencing lion movements and habitat use in the western Serengeti ecosystem, Tanzania. Sci. Rep. 12, 18890 (2022).

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19. C. E. Searle, J. B. Smit, J. J. Cusack, P. Strampelli, A. Grau, L. Mkuburo, D. W. Macdonald, A. J. Loveridge, A. J. Dickman, Temporal partitioning and spatiotemporal avoidance among large carnivores in a human-impacted African landscape. PLoS One. 16, 1–20 (2021).
20. G. Spong, Space use in lions, Panthera leo, in the Selous Game Reserve: Social and ecological factors. Behav. Ecol. Sociobiol. 52, 303–307 (2002).
21. J. P. Suraci, L. G. Frank, A. Oriol-Cotterill, S. Ekwanga, T. M. Williams, C. C. Wilmers, Behavior-specific habitat selection by African lions may promote their persistence in a human-dominated landscape. Ecology. 100, e02644 (2019).
22. M. Valeix, G. Hemson, A. J. Loveridge, G. Mills, D. W. Macdonald, Behavioural adjustments of a large carnivore to access secondary prey in a human-dominated landscape. J. Appl. Ecol. 49, 73–81 (2012).
23. L. K. Van Der Weyde, C. Mbisana, R. Klein, Multi-species occupancy modelling of a carnivore guild in wildlife management areas in the Kalahari. Biol. Conserv. 220, 21–28 (2018).

Appendix C: Supplementary Tables and Figures for Chapter III

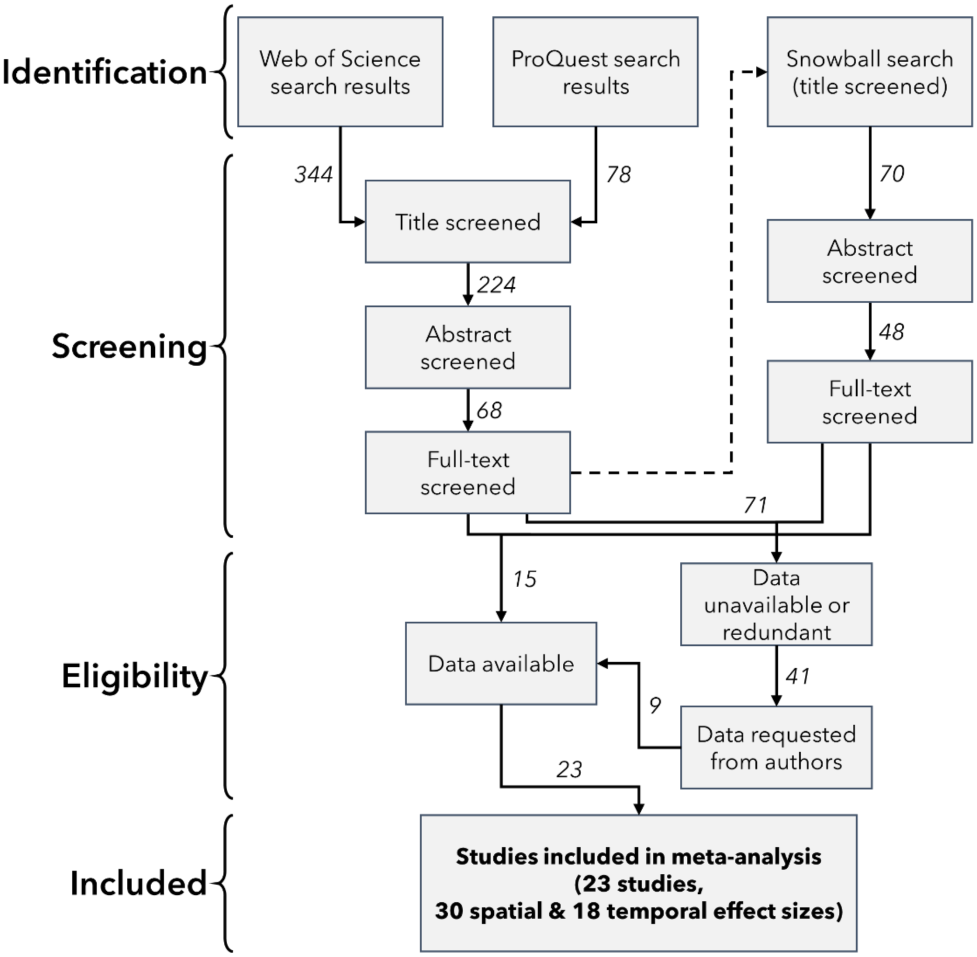

Figure S3-1: Flow chart outlining the procedure for identifying and including relevant studies for use in the meta-analysis. Numbers indicate the number of publications produced by the preceding step that were used in the subsequent step (e.g., Web of Science search resulted in 344 publications that were then screened based on the publication title).

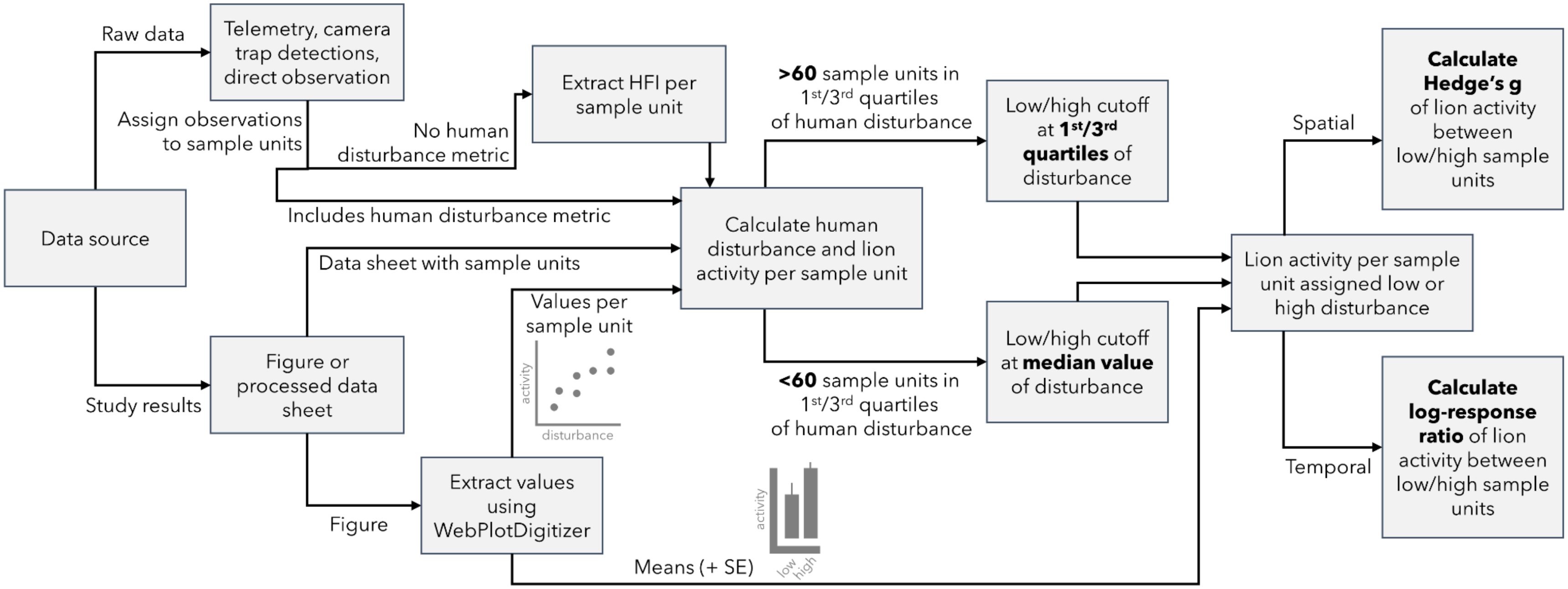

Figure S3-2: Decision tree chart illustrating the process for extracting lion activity and human disturbance data from included studies

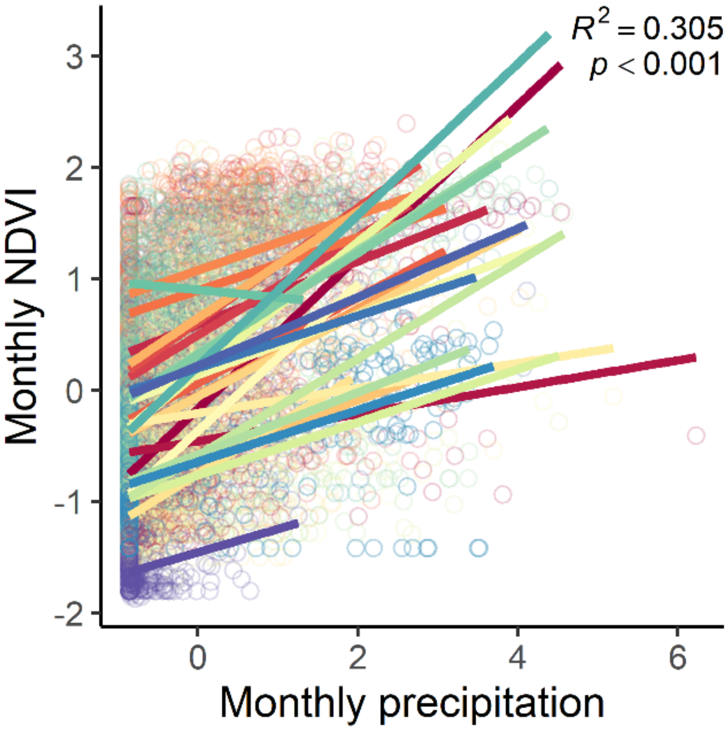

Figure S3-3: Relationship between monthly average precipitation and Normalized Difference Vegetation Index (NDVI) values at African study sites between 2000-2019. Each line represents the linear model for a study site, each point a monthly value of precipitation and NDVI. A linear model including study site as an interaction term with NDVI indicated significant positive relationships between monthly NDVI and precipitation at all but one study site (see Table S3-4 for correlation coefficients by study site).

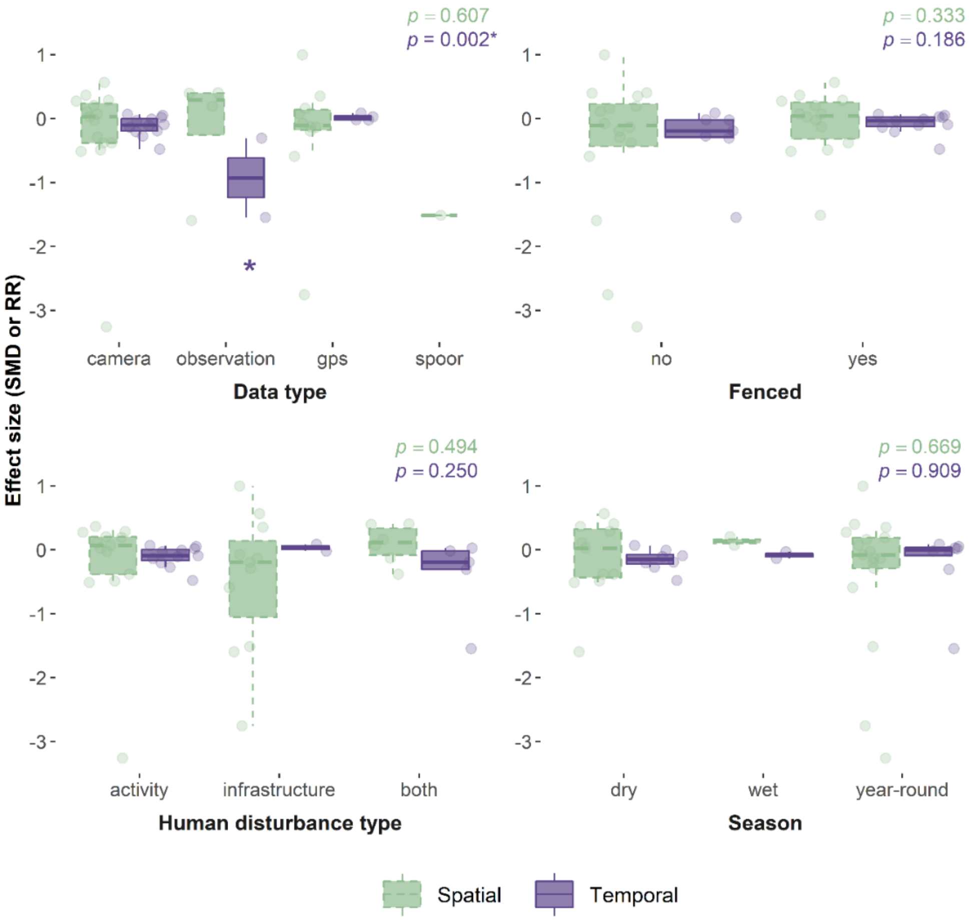

Figure S3-4: Distribution of effect sizes of lion responses to human disturbance by categorical study characteristics: the type of lion observation data based on methods used to monitor lions, whether the study area was fenced or un-fenced, the type of human disturbance that was measured in the study and/or used to calculate effect sizes, and the period of the year in which lions were monitored. Negative values on both y-axes indicate lion avoidance of human disturbance in time and space. All variables are scaled and centered. *P*-values show the result of ANOVA tests of the variables on spatial (green) and temporal (purple) effect sizes, and significant effects ($p < 0.05$) are denoted by a star. The human footprint was considered to represent 'both' types of human disturbance, because the metric is a combination of many human disturbances, including human population size, land use types, and built infrastructure. SMD = standardized mean difference; RR = log response ratio.

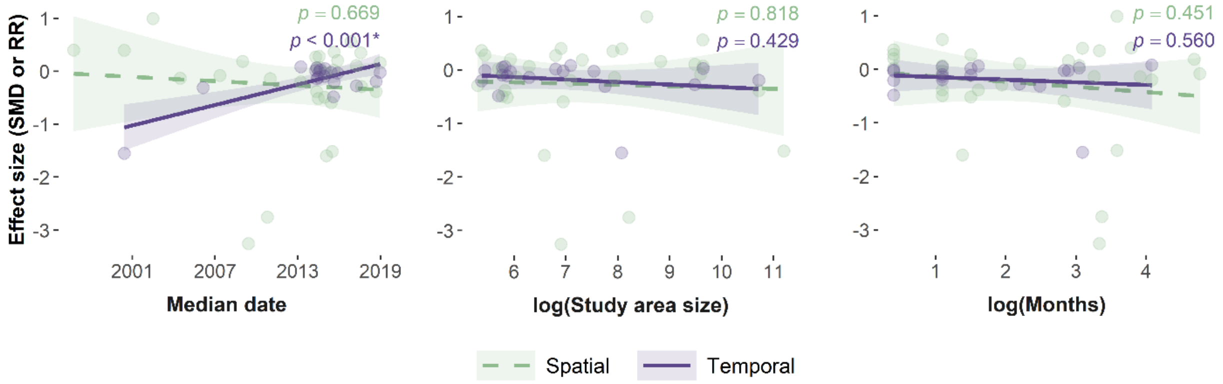

Figure S3-5: Distribution of effect sizes of lion responses to human disturbance by continuous study characteristics: the median date of the study period, the log-transformed size of the study area measured in sq-km, and the log-transformed duration of the study period in months. Negative values on both y-axes indicate lion avoidance of human disturbance in time and space. All variables are scaled and centered. *P*-values show the result of linear models for each variable's relationship with spatial (green) and temporal (purple) effect sizes, and significant effects ($p < 0.05$) are denoted by a star. SMD = standardized mean difference; RR = log response ratio.

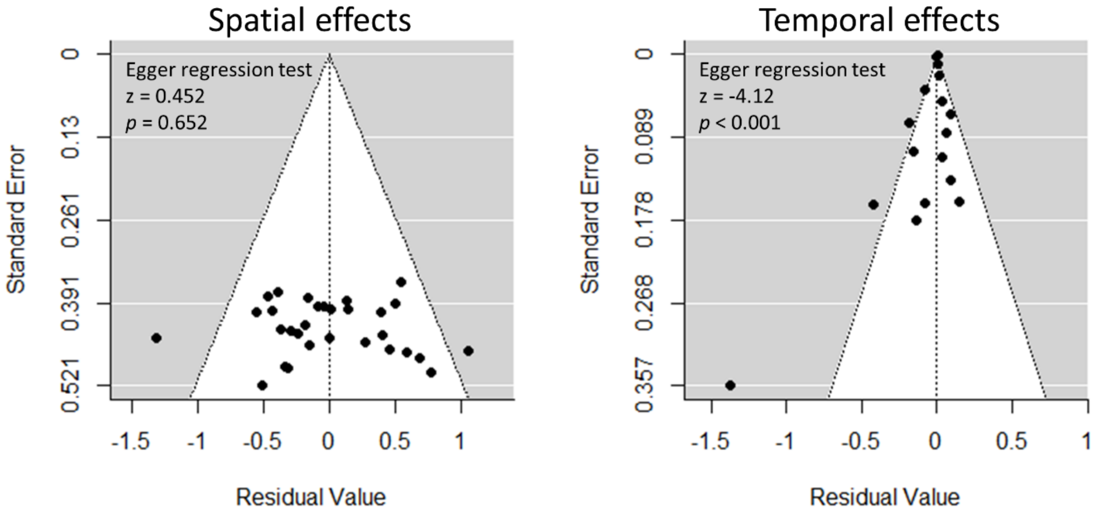

Figure S3-6: Funnel plots for the lowest AICc mixed-effects models of lion spatial and temporal responses to human disturbance, comparing the effect size residuals to their corresponding sampling variance. Egger regression tests were used to test funnel plot asymmetry to check for possible publication bias.

Table S3-1: Descriptions of the locations and study periods for each study site included in the meta-analysis.

Study reference (ID)	Study area	Country	Study area size (km^2)	Latitude, Longitude	Season	Study period	Duration (months)
Beukes et al. 2017 (1)	Kgalagadi Transfrontier Park	South Africa	15,396	-25.38, 20.38	year-round	2013-2015	21
Chaudhary et al. 2020 (2)	Gir Protected Area	India	200	21.14, 70.83	year-round	2017-2018	7
Dolrenry 2013 (3)	Amboseli-Tsavo Ecosystem	Kenya	3,684	-2.63, 37.26	year-round	2009-2011	29
Droge et al. 2020 (4)	Kafue National Park	Zambia	2,702	-14.43, 25.93	year-round	2016-2018	28
Droge et al. 2017 (5)	Liuwa Plain National Park	Zambia	1,200	-14.5, 22.5	year-round	2010-2015	59
Everatt et al. 2019 (6)	Greater Limpopo Transfrontier Conservation Area	Mozambique	73,000	-22.93, 32.31	year-round	2014-2016	36
Gogoi et al. 2020 (7)	Gir Protected Area	India	725	21.14, 70.83	dry	2014-2015	4
Green et al. 2018 (8)	Masai Mara National Reserve	Tanzania	1,500	-1.47, 35.07	year-round	2004-2013	108
Hayward & Hayward 2006 (9)	Addo Elephant National Park	South Africa	420	-33.47, 25.75	year-round	2003-2005	26
Loveridge et al. 2017 (10)	Hwange National Park	Zimbabwe	14,650	-19, 26.5	year-round	2002-2012	117
Maddox 2003 (11)	Serengeti-Mara ecosystem	Tanzania	3,200	-2.61, 35.22	year-round	1999-2001	22
Miller et al. 2018 (12)	Hluhluwe-iMfolozi Park	South Africa	900	-28.22, 31.95	year-round	2013-2015	4.5
	KwaZulu Private Game Reserve	South Africa	377	-27.57, 31.66	wet	2015	1.5
	Makalali Private Game Reserve	South Africa	323	-24.21, 30.63	year-round	2014-2015	3
	Phinda Private Game Reserve	South Africa	230	-27.81, 32.35	dry	2014	1.5
	Tembe Elephant Park	South Africa	299	-26.95, 32.44	dry	2015	1.5
	Timbavati Private Game Reserve	South Africa	541	-24.4, 31.31	wet	2013-2014	3

Miller et al. 2018 (12)	uMkhuze Game Reserve	South Africa	353	-27.65, 32.15	dry	2013-2015	4.5
	Venetia-Limpopo Nature Reserve	South Africa	321	-22.35, 29.31	dry	2014-2015	3
	Welgevonden Private Game Reserve	South Africa	339	-24.31, 27.83	dry	2013-2015	5
	Zululand Rhino Reserve	South Africa	216	-27.77, 32.11	dry	2015	1.5
Mills et al. 2020 (13); Mills & Harris 2020 (14)	W-Arly-Pendjari	Burkina Faso, Niger	13,100	11.5, 1.5	dry	2016-2018	9
Mogensen et al. 2011 (15)	Masai Mara National Reserve and Koyaki Ranch	Kenya	2,323	11.5, 1.5	year-round	2005-2006	12
Oriol-Cotterill et al. 2015 (16)	Laikipia County	Kenya	2,800	-1.44, 35.21	year-round	2009-2012	50
Schooler et al. 2022 (17)	Serengeti ecosystem	Tanzania	6,800	-2.67, 34.58	year-round	2018-2019	18
Schuette et al. 2013 (18)	Southern Rift Valley	Kenya	1,000	0.57, 36.67	year-round	2008-2010	28
Searle et al. 2021 (19)	Ruaha-Rungwa Landscape	Tanzania	45,000	-1.92, 36.13	dry	2018-2019	6
Spong 2002 (20)	Selous Game Reserve	Tanzania	1,000	-7.4, 34.8	dry	1994-1999	44
Suraci et al. 2019 (21)	Laikipia District	Kenya	1,040	-7.58, 38.25	year-round	2014-2016	17
Valeix et al. 2012 (22)	Makgadikgadi Pans National Park	Botswana	5,200	0.44, 36.81	year-round	2001-2003	36
Van der Weyde et al. 2018 (23)	Okwa Wildlife Management Area	Botswana	15,290	-20.5, 23	dry	2016	3

Table S3-2: Descriptions of lion and human data and method of data extraction for each study included in the meta-analysis. In data extraction descriptions: S = spatial data extraction, T = temporal data extraction, HFI = human footprint index.

Study (ID)	Data type	Lion activity metric	Human disturbance metric	Data extraction description	ES type	ES	Var.	Low disturbance		High disturbance	
								Mean (SD)	N	Mean (SD)	N
Beukes et al. 2017 (1)	GPS	detections	human footprint	Created grid across lion locations using average daily displacement for grid size (~4.9-km), designated grid cells as low/high human disturbance based on average HFI value per grid cell (1st/3rd quartiles). *S:* Calculated average number of observations per grid cell. *T:* Calculated the proportion of fixes representing active lion movement during day/night.	SMD	0.07	0.021	191.76 (290.06)	96	222.38 (520.37)	96
					RR	0.03	0.000	0.76	3402	0.74	3929
Chaudhary et al. 2020 (2)	camera	detections	distance to residential	Sample units assigned low/high human disturbance using average distance to settlement. Calculated average number of lion observations per camera station.	SMD	-0.29	0.081	5.16 (6.18)	31	3.24 (7.06)	21
Dolrenry 2013 (3)	GPS, observation	occupancy	building density	Lion occupancy was extracted from 44 equidistant points along line in Figure 3.3, using WebPlotDigitizer. Lion density was assigned to high/low categories based on median boma density.	SMD	-2.75	0.170	0.88 (0.05)	22	0.61 (0.12)	24
Dröge et al. 2020 (4)	GPS	detections	human footprint	Converted lion tracks from supplemental data to points at track vertices. Created 1000m grid across	SMD	0.35	0.008	3.59 (3.73)	244	6.16 (9.63)	244

				lion locations, calculated average number of observations per grid cell, designated lion locations as low/high human disturbance based on average HFI value per grid cell (1st/3rd quartiles).							
Dröge et al. 2017 (5)	GPS	GPS locations	distance to residential	Created 1000m grid across lion locations, used 1st and 3rd quartiles of distance to village for low/high disturbance categories. *S:* Calculated average number of fixes and their distances to village within each grid cell *T:* Calculated the proportion of fixes representing active lion movement during day/night.	SMD	-0.20	0.010	11.27 (37.66)	202	5.73 (13.06)	201
					RR	0.09	0.001	0.83	1167	0.77	473
Everatt et al. 2019 (6)	spoor	occupancy	distance to residential	Averaged lion occupancy across sample units; sample units assigned high/low human disturbance using median of distance to village variable.	SMD	-1.51	0.050	0.67 (0.21)	52	0.28 (0.3)	51
Gogoi et al. 2020 (7)	observation	spatial density	distance to residential	Lion density and distance to human habitation values extracted from Fig S5. Sample units assigned high/low human disturbance using 1st and 4th quartiles of distance to habitation variable. Calculated average lion density for high/low categories.	SMD	-1.60	0.066	0.41 (0.84)	40	-0.87 (0.74)	40

Green et al. 2018 (8)	observation	detections	land use type	Designated Talek West as high disturbance, other areas as low disturbance based on site descriptions in text. Created 1000m grid across lion locations, calculated average number of observations per 100 sample days per grid (4 years for low disturbance, 7 years for high disturbance based on text descriptions).	SMD	0.19	0.018	0.44 (0.67)	137	0.6 (1.04)	94
Hayward & Hayward 2006 (9)	GPS	detections	human footprint	Created grid across lion locations based on avg daily displacement (~5.5-km), designated grid cells as low/high human disturbance based on average HFI value per grid cell (1st/3rd quartiles). Calculated average number of lion observations per grid cell.	SMD	-0.13	0.020	17.18 (18.58)	96	14.68 (19.24)	110
Loveridge et al. 2017 (10)	GPS	space use	distance to residential	Designated low/high disturbance using median distance to village (22714m). Calculated the average the number of observations among individuals in low vs high human disturbance locations.	SMD	-0.08	0.032	16.69 (12.49)	62	15.71 (12.52)	62
Maddox 2003 (11)	observation	density, behavioral observations	land use type	Characterized Loliondo as high human disturbance and NCA and Serengeti as low human disturbance based on site descriptions in text. *S:* Extracted	SMD	0.40	0.021	0.28 (0.1)	70	0.32 (0.13)	152

				average lion densities (SE) from Figure 26, calculated SD using sample sizes in text. *T:* Extracted sample sizes and proportion active from Figure 41, converted proportions to counts to calculate proportion nocturnal activity.	RR	-1.55	0.129	0.17	47	0.80	10
Miller et al. 2018 (12)	camera	detections	human trap success	Calculated trap success (detections/100 trap-nights) for humans & lions for each camera stations from supplemental raw data. Camera stations assigned low/high human disturbance using median values of human trap-success. *S:* Lion trap success averaged for disturbance categories. *T:* Calculated the proportion of lion detections during day/night.	SMD	0.27[1]	0.054	7.17 (7.1)	32	9.9 (11.45)	45
						0.20[2]	0.097	4.2 (5.13)	29	5.98 (12.79)	16
						-0.03[3]	0.052	22.5 (25.55)	38	21.77 (29.07)	39
						0.28[4]	0.097	4.84 (8.09)	23	7.42 (9.76)	19
						0.03[5]	0.126	11.67 (8.45)	15	11.9 (9.22)	17
						0.07[6]	0.061	3.16 (6.11)	31	3.53 (4.51)	35
						-0.51[7]	0.042	2.92 (5.57)	53	0.71 (1.74)	45
						-0.49[8]	0.063	5.38 (4.9)	33	3.23 (3.7)	32
						-0.38[9]	0.041	7.53 (7.09)	54	4.76 (7.32)	45
						0.37[10]	0.136	4.39 (6.22)	15	13.48 (33.65)	15

					RR	0.02[1]	0.003	0.85	101	0.84	196
						-0.03[2]	0.020	0.66	56	0.68	44
						0.05[3]	0.004	0.63	288	0.60	286
						-0.01[4]	0.013	0.73	49	0.74	62
						-0.48[5]	0.027	0.39	77	0.63	89
						-0.14[6]	0.011	0.72	50	0.83	63
						-0.11[7]	0.002	0.90	68	1.00	14
						-0.10[8]	0.006	0.81	79	0.89	46
						0.07[9]	0.007	0.69	207	0.64	109
						-0.20[10]	0.029	0.59	29	0.72	89
Mills et al. 2020 (13)	camera	occupancy	occupancy	Camera grids were designated as being in low or high human disturbance sites according to human disturbance designations in Mills & Harris 2020 (15). Calculated average lion occupancy between low/high disturbance grids.	SMD	0.11	0.020	0.56 (0.24)	94	0.58 (0.25)	110
Mills & Harris 2020 (14)	camera	detections	occupancy	Calculated the proportion of lion detections during day/night between low and high human camera stations designated in study. Nocturnal times determined as described in the study text. Uses same raw data set as Mills et al. 2020 (13)	RR	-0.27	0.032	0.53	36	0.69	62
Mogensen et al. 2011 (15)	observation	activity type	land use type	Designated pride A and B as low disturbance, pride C as high disturbance based on study site descriptions in text. Calculated	RR	-0.31	0.038	0.66	16	0.90	18

				number of active and nocturnal detections from Figure 2.							
Oriol-Cotterill et al. 2015 (16)	GPS	detections	distance to boma	Extracted and pooled means and SE of distance to boma at 1200 (high human disturbance) and between 2300-0500 (low human disturbance) in Fig. 3-3. Sample sizes calculated from total # fixes reported, divided by 2 into seasons, then divided into equal numbers of fixes per hour reported. Values inverted to represent lion use and avoidance in accordance with ES interpretations.	SMD	-0.14	0.001	-2.86 (2.7)	13404	-3.2 (0.29)	2234
Schooler et al. 2022 (17)	GPS	detections	human footprint	Created grid across lion locations using average daily displacement for grid size (~2.3-km), designated grid cells as low/high human disturbance based on average HFI value per grid cell (1st/3rd quartiles). *S:* Calculated average number of observations per grid cell. *T:* Calculated the proportion of fixes representing active lion movement during day/night.	SMD	0.16	0.012	109.91 (232.8)	166	154.11 (304.66)	166
					RR	-0.02	0.000	0.63	2953	0.65	3531
Schuette et al. 2013 (18)	camera	occupancy	land use type	Designated 'CCS' site as low disturbance and 'Grazing Area' site as high disturbance based on site descriptions in text. Extracted the lion occupancy mean and SD for both sites in Figure 4b.	SMD	-3.26	0.097	0.67 (0.27)	40	0.08 (0.06)	57

Searle et al. 2021 (19)	camera	detections	land use type	Classified MBOMIPA WMA as high human disturbance and other sites as low disturbance based on text descriptions. 'Ruaha NP miombo woodland' survey was excluded from analysis because of data issue discussed in text. *S:* Calculated average lion trap success per camera station in low vs. high sample units. *T:* Calculated proportion of lion detections in day/night.	SMD	-0.38	0.082	21.26 (18.2)	67	14.56 (12.58)	15
					RR	-0.19	0.000	0.82	598	1.00	83
Spong 2002 (20)	observation	detections	human footprint	Created 1000m grid across lion locations, and designated grid cells as low/high human disturbance based on the median (among grid cells) of average within-grid cell HFI value. Calculated average number of lion observations per grid cell.	SMD	0.40	0.025	2.29 (2.03)	108	3.64 (4.77)	67
Suraci et al. 2019 (21)	GPS	detections	distance to boma	Created grid across lion locations using average daily displacement for grid size (~3-km), designated grid cells as low/high human disturbance based on average distance to nearest boma per grid cell (1st/3rd quartiles). *S:* Calculated average number of observations per grid cell *T:* Calculated the proportion of fixes representing active lion movement during day/night, as designated by the study text definition of nighttime from 08:00 and 18:00.	SMD	-0.59	0.037	1666.21 (1602.08)	57	719.23 (1571.85)	57
					RR	-0.02	0.000	0.93	2308	0.95	1032

Valeix et al. 2012 (22)	GPS	Jacob's index	distance to boma	Designated 0-6km from cattle-posts as high and >6km as low disturbance based on text descriptions. Extracted mean and 95%CI of Jacob's index of selection, calculated SD from sample sizes described in text.	SMD	1.00	0.069	-0.42 (0.37)	18	-0.02 (0.39)	108
Van der Weyde et al. 2018 (23)	camera	detections	distance to residential	Designated camera stations as low/high human disturbance based on median distance from village. Calculated lion trap success (detections/100 trap-nights) for camera stations from raw data.	SMD	0.56	0.043	0.18 (0.69)	48	1.8 (4.0)	48

Sites in Miller et al. 2018: [1]Hluhluwe-iMfolozi Park, [2]KwaZulu Private Game Reserve, [3]Makalali Private Game Reserve, [4]Phinda Private Game, Reserve, [5]Tembe Elephant Park, [6]Timbavati Private Game Reserve, [7]uMkhuze Game Reserve, [8]Venetia-Limpopo Nature Reserve, [9]Welgevonden Private Game Reserve, [10]Zululand Rhino Reserve

Table S3-3: Top-performing mixed-effects models and global models used to assess the effects of ecological and anthropogenic local conditions on the magnitude of lion responses (SMD and RR) to human disturbance, with model evaluation parameters and estimated coefficients of model variables. All models within 2 ΔAICc from the lowest AIC$_c$ model were included in the final model set (also used for weighted model averaging [Table S2]). SMD$_w$ = average weighted standardized mean difference (REM intercept); RR$_w$ = average weighted log response ratio (REM intercept); HFI$_{sp}$ = spatial variation in human footprint index; CAT$_a$ = average cattle production; NDVI$_{sp}$ = average spatial variation in NDVI; NDVI$_{tm}$ = temporal variation in NDVI; NDVI$_a$ = average overall NDVI. *coefficient 95% CI significantly different from 0.

							Model Coefficients (95% CI)						
Mixed-effects models	**AIC$_c$**	**ΔAIC$_c$**	**Model weight**	***R²***	**$\hat{\tau}^2$ 95% CI**	**I^2 95% CI**	**Average ES**	HFI_a	HFI_{sp}	CAT_a	$NDVI_a$	$NDVI_{tm}$	$NDVI_{sp}$
Spatial responses							**SMD$_w$**						
$HFI_{sp} + NDVI_{sp} + NDVI_{tm}$	52.95	0	0.45	0.76	0.108- 0.449	82.2- 95.0%	-0.268* (-0.433, -0.103)	-	0.286* (0.004, 0.092)	-	-	0.218* (0.034, 0.402)	-0.893* (-1.114, -0.671)
$HFI_{sp} + CAT_a + NDVI_{sp} + NDVI_{tm}$	53.34	0.38	0.37	0.79	0.099- 0.432	80.6- 94.8%	-0.279* (-0.437, -0.121)	-	0.243* (0.052, 0.434)	-0.158 (-0.339, 0.024)	-	0.235* (0.059, 0.411)	-0.820* (-1.048, -0.592)
$HFI_{sp} + NDVI_{sp}$	54.79	1.83	0.18	0.69	0.132- 0.491	85.0- 95.5%	-0.254* (-0.437, -0.071)	-	0.245* (0.034, 0.457)	-	-	-	-0.819* (-1.050, -0.589)
Global Model	59.58	6.63		0.76	0.105- 0.474	80.3- 94.9%	-0.267* (-0.431, -0.103)	-0.081 (-0.262, 0.100)	0.233* (0.041, 0.426)	-0.162 (-0.347, 0.022)	-0.021 (-0.192, 0.151)	0.236* (0.056, 0.416)	-0.783* (-1.049, -0.517)
Temporal responses							**RR$_w$**						
$HFI_{sp} + CAT_a + NDVI_a + NDVI_{sp}$	-6.29	0	0.32	1	0.007- 0.251	66.7- 98.7%	-0.068* (-0.104, -0.033)	-	0.061* (0.039, 0.084)	-0.102* (-0.160, -0.044)	-0.015* (-0.027, -0.002)	-	-0.061* (-0.076, -0.045)
$HFI_{sp} + CAT_a + NDVI_{sp}$	-6.12	0.17	0.29	0.95	0.005- 0.219	73.1- 99.1&	-0.075* (-0.115, -0.036)	-	0.056* (0.028, 0.084)	-0.118* (-0.175, -0.061)	-	-	-0.053* (-0.073, -0.032)
CAT_a	-5.42	0.87	0.2	0.38	0.006- 0.183	81.7- 99.3%	-0.089* (-0.142, -0.036)	-	-	-0.095* (-0.160, -0.029)	-	-	-
$CAT_a + NDVI_{sp}$	-5.27	1.02	0.19	0.61	0.005- 0.189	76.4- 99.2%	-0.07* (-0.119, -0.021)	-	-	-0.074* (-0.134, -0.015)	-	-	-0.037* (-0.075, -0.001)
Global Model	5.84	12.13		0.62	0.006- 0.293	61.2- 98.7%	-0.026 (-0.066, 0.013)	0.013 (-0.016, 0.042)	0.046* (0.016, 0.077)	-0.089* (-0.151, -0.028)	-0.022* (-0.039, -0.005)	0.034 (-0.023, 0.092)	-0.058* (-0.081, -0.035)

Table S3-4: Results of tests of correlation between monthly precipitation vs. NDVI at African study sites. Study sites in Gir National Forest, India, were excluded due to the spatial extent of the monthly precipitation data. *Pearson's *r* coefficient *p*-value < 0.05.

Study site (Study ID)	Study period	Pearson's *r*	*p*-value
Addo Elephant National Park (9)	2003-2005	-0.055	0.387
Amboseli-Tsavo Ecosystem (3)	2009-2011	0.379*	<0.001
Greater Limpopo Transfrontier Conservation Area (6)	2014-2016	0.262*	<0.001
Hluhluwe-iMfolozi Park (12)	2013-2015	0.350*	<0.001
Hwange National Park (10)	2002-2012	0.631*	<0.001
Kafue National Park (4)	2016-2018	0.683*	<0.001
Kgalagadi Transfrontier Park (1)	2013-2015	0.326*	<0.001
KwaZulu Private Game Reserve (12)	2015	0.498*	<0.001
Laikipia County (16)	2009-2012	0.154*	0.014
Laikipia District (21)	2014-2016	0.192*	0.002
Liuwa Plain National Park (5)	2010-2015	0.576*	<0.001
Makalali Private Game Reserve (12)	2014-2015	0.346*	<0.001
Makgadikgadi Pans National Park (22)	2001-2003	0.567*	<0.001
Masai Mara National Reserve and Koyaki Ranch (15)	2005-2006	0.336*	<0.001
Masai Mara National Reserve (8)	2004-2013	0.354*	<0.001
Okwa Wildlife Management Area (23)	2016	0.484*	<0.001
Phinda Private Game Reserve (12)	2014	0.278*	<0.001
Ruaha-Rungwa Landscape (19)	2018-2019	0.733*	<0.001
Selous Game Reserve (20)	1994-1999	0.579*	<0.001
Serengeti ecosystem (17)	2018-2019	0.582*	<0.001
Serengeti-Mara ecosystem (11)	1999-2001	0.499*	<0.001
Southern Rift Valley (18)	2008-2010	0.418*	<0.001
Tembe Elephant Park (12)	2015	0.329*	<0.001
Timbavati Private Game Reserve (12)	2013-2014	0.353*	<0.001
uMkhuze Game Reserve (12)	2013-2015	0.428*	<0.001
Venetia-Limpopo Nature Reserve (12)	2014-2015	0.319*	<0.001
W-Arly-Pendjari (13, 14)	2016-2018	0.794*	<0.001
Welgevonden Private Game Reserve (12)	2013-2015	0.498*	<0.001
Zululand Rhino Reserve (12)	2015	0.406*	<0.001

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