

REVIEW

The influence of human activity on predator–prey spatiotemporal overlap

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Abstract

1. Despite growing evidence of widespread impacts of humans on animal behaviour, our understanding of how humans reshape species interactions remains limited.
2. Here, we present a framework that draws on key concepts from behavioural and community ecology to outline four primary pathways by which humans can alter predator–prey spatiotemporal overlap.
3. We suggest that predator–prey dyads can exhibit similar or opposite responses to human activity with distinct outcomes for predator diet, predation rates, population demography and trophic cascades. We demonstrate how to assess these behavioural response pathways with hypothesis testing, using temporal activity data for 178 predator–prey dyads from published camera trap studies on terrestrial mammals.
4. We found evidence for each of the proposed pathways, revealing multiple patterns of human influence on predator–prey activity and overlap. Our framework and case study highlight current challenges, gaps, and advances in linking human activity to animal behaviour change and predator–prey dynamics.
5. By using a hypothesis-driven approach to estimate the potential for altered species interactions, researchers can anticipate the ecological consequences of human activities on whole communities.

KEYWORDS

animal behaviour, human activity, predator–prey, prey refuge, spatiotemporal overlap, trophic cascades

1 | INTRODUCTION

Human activity can alter the behaviour of animals by amplifying or dampening perceptions of risk, food availability, or safety (Gaynor et al., 2019; Geffroy et al., 2020; Hammond et al., 2020; Sih et al., 2011). Yet, complex behavioural feedbacks among multiple ecological players (i.e. predators, prey, competitors) have limited our ability to establish links between human-altered animal behaviour

and broader ecological change, such as altered predator diet, predation rate, population demography, competitive exclusion, or trophic cascades. Although human activity—defined broadly here as human presence and infrastructure—is known to affect animal populations by changing species interactions, including predation (Gaynor et al., 2021), knowledge of these dynamics is largely anecdotal or context-specific (Wilson et al., 2020). Formally recognizing the effect of humans on predator–prey interactions is necessary to align

hypothesis testing with the range of potential effects of increasing human activity on the persistence and coexistence of wild animals (Mumma et al., 2018; Sinclair et al., 2003).

The field of behavioural ecology has long demonstrated that predators and prey influence each other's spatial distributions (Brown et al., 1999; MacArthur & Pianka, 1966) in a behavioural response race, whereby predators seek to encounter prey while prey seek to avoid predators (Lima & Dill, 1990; Sih, 1984). Considerable research has established that contextual factors (e.g. patch size, habitat complexity, resources, and species functional traits) can give an advantage to either player in the predator–prey response race (Fretwell, 1972; Laundré, 2010; Luttbeg et al., 2020; Schmidt & Kuijper, 2015; Sih et al., 1998; Smith et al., 2019). These conceptual models have allowed ecologists to predict changes to the consumptive (e.g. predation) and non-consumptive (e.g. risk effects) dynamics of ecological communities. However, although classic behavioural response models have been extended to communities with multiple predators (Sih et al., 1998) surprisingly few models have been broadened to describe how human activity influences the contest between predator and prey (but see Miller & Schmitz, 2019 and Muhly et al., 2011).

Understanding how human activity affects animal behaviour and species interactions is complex because animal responses to humans are rarely uniform. Many wild animals avoid humans by changing patterns of movement, activity, or consumption (Gaynor et al., 2018; Smith et al., 2015; Tucker et al., 2018), whereas others preferentially use settings of human activity to gain resources or safety (Berger, 2007; Geffroy et al., 2015; Newsome & Van Eeden, 2017). Accounting for this variation in animal responses could be key to anticipating shifts in predation and potential cascading trophic effects (Kuijper et al., 2016; Yovovich et al., 2021). Each player's (i.e. predator or prey) response to humans can vastly influence the ecological outcome. For example, if a predator avoids human activity but its prey does not, predator and prey may encounter each other less often (Berger, 2007; Rogala et al., 2011), possibly reducing predation and/or non-consumptive effects. Alternatively, if both predator and prey perceive human activity as a threat, mutual avoidance of humans may force prey and predator to share space and time. The loss of spatiotemporal refuges that previously stabilized predator–prey coexistence (Schoener, 1974; Shammoo et al., 2018), may lead to the increase of predation and its non-consumptive effects.

Here, we present a framework that draws on theory and empirical literature to conceptualize the behavioural pathways by which human activity can reshape the overlap between predators and prey. As a proof of concept, we review the literature to evaluate evidence for each pathway in terrestrial mammal predator–prey dyads, and conduct an analysis to test how human activity influenced predator–prey temporal overlap. Further, we highlight current challenges, gaps and advances in linking animal behaviour change to predator–prey interactions and ecological dynamics in settings with human activity. Our goal is to provide a testable framework that allows researchers to evaluate hypotheses and assess the potential for human-altered species interactions.

2 | HUMAN-ALTERED PREDATOR–PREY OVERLAP

Humans are dominant actors in ecological communities around the world. Human presence and infrastructure, which we collectively refer to as human activity, alter sensory stimuli that animals may perceive as associated with risk or reward (e.g. smell, sound, light, movement; Dittmer et al., 2021; Francis & Barber, 2013). Varied stimuli can differentially reshape animals' perceptions of risk–reward trade-offs. For instance, different types of human activity can influence species differently, as when large mammal predators spatially avoided building density and temporally avoided human presence, whereas smaller mammal predators temporally avoided human presence but did not spatially avoid building density (Nickel et al., 2020). Animals may also only perceive altered risk–reward cues at a certain threshold of human activity. For instance, mule deer *Odocoileus hemionus* rarely used areas with greater than 3% surface disturbance from energy development during migration (Sawyer et al., 2020). An animal's experience with human activity (e.g. prior events, duration of exposure) and its functional traits (e.g. body size, propensity for learning, memory, boldness) may also influence perception of risk–reward cues and its corresponding behavioural response (Moiron et al., 2020; Ross et al., 2019). For instance, many species have learned to associate human activity with increased foraging opportunities (e.g. garbage, agriculture; Newsome et al., 2015).

In response to risk–reward cues, animals can adjust their spatial distribution or temporal activity to avoid or seek out human activity. If individuals in a given animal population consistently alter their spatio-temporal distribution, we might expect reverberating impacts on closely interacting species, such as predators and their prey (Muhly et al., 2011; Wilson et al., 2020). Because predators and their prey can each respond to human activity along a continuum of attraction to avoidance, there are four behavioural pathways by which humans can increase or decrease predator–prey spatiotemporal overlap (hereafter, 'overlap'; Figure 1). Changing the degree of overlap between predator and prey may tip the behavioural response race in favour of one player to affect consumptive or non-consumptive dynamics. Although linking predator–prey overlap to predation requires evaluating the full predation sequence (i.e., the encounter, pursuit, and successful capture of prey; Guiden et al., 2019; Lima & Dill, 1990; Suraci et al., 2022; Wootton et al., 2021), a predator and prey first must occupy the same space at the same time for an encounter to occur. We reduce this complexity to consider overlap a necessary precursor to any predator–prey encounter (Prugh et al., 2019). While human activity can also change the densities of both predator and prey species through non-behavioural pathways (e.g. direct mortality, habitat degradation), here we focus on behaviourally mediated effects of humans on predators and prey.

2.1 | Human activity increases predator–prey overlap

There are two behavioural pathways through which human activity can increase the overlap between a predator and its prey,

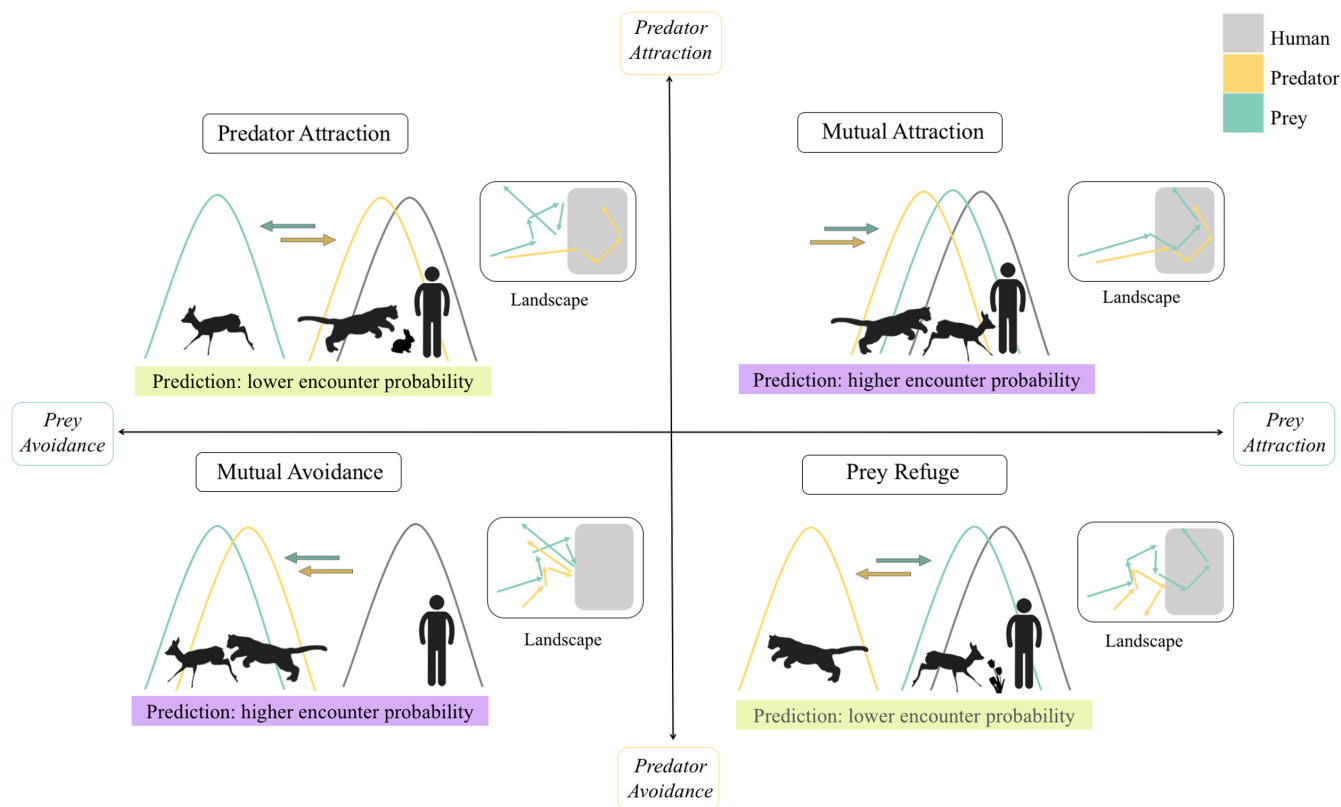


FIGURE 1 Humans can alter predator and prey behaviour, spatiotemporal overlap and encounter probability via four major pathways: mutual attraction, mutual avoidance, prey refuge, and predator attraction. Predator (y-axis) and prey (x-axis) respond to human activity along a continuum of attraction to avoidance. Similar responses of predator and prey to human activity are predicted to result in increased predator–prey overlap and possible encounters, whereas opposite responses are predicted to reduce overlap and possible encounters.

potentially tipping the behavioural response race in favour of the predator. First, **mutual attraction** to human activity (i.e. synanthropy) may increase predator–prey encounter rates (Figure 1, quadrant I). For example, the attraction of black bears *Ursus americanus* to human-associated food led to increased predation of mutually attracted red-backed voles *Clethrionomys gapperi* feeding nearby (Morris, 2005). Second, **mutual avoidance** of human activity may cause a predator and prey to increase overlap to avoid a shared perceived risk (Figure 1, quadrant III). For instance, in Manas National Park, India, tigers *Panthera tigris* and ungulate prey constrained their spatiotemporal activity to avoid humans in the park, thus increasing overlap with one another (Lahkar et al., 2020). If mutual attraction or mutual avoidance transpire in both space and time, the realized niche (Hutchinson, 1957) between predator and prey will be compressed and encounter rates may be amplified. This change may lead to increased predation rates or phenomena such as ecological traps (Gates & Gysel, 1978).

2.2 | Human activity decreases predator–prey overlap

There are two behavioural pathways by which human activity can decrease the overlap between a predator and its prey, potentially

tipping the behavioural response race in favour of prey. First, predators may avoid human activity while prey do not, creating a spatial or temporal **prey refuge** (Figure 1, quadrant IV; Berger, 2007; Muhly et al., 2011). Prey refuges (also called ‘human shields’) occur in environments where the absence of large predators for fear of people allows prey species to reduce their anti-predator behaviour (Shannon et al., 2014) or selectively use human-occupied habitats that predators avoid (Gaynor et al., 2022). Second, prey may avoid human activity while predators do not (Fleming & Bateman, 2018). This case may entail **predator attraction** (Figure 1, quadrant II), whereby predators select settings of high human activity, affording human-avoidant prey a refuge. Predator use of human settings may be driven by prey switching and the selection for synanthropic or domestic prey, or other human food subsidies, such as garbage or agriculture (Murdoch, 1969; Murdoch & Oaten, 1975; Newsome et al., 2015). For instance, in Maharashtra, India, 87% of leopard *Panthera pardus* diet in human-dominated areas consisted of domestic animals, reducing consumption of wild species (Athreya et al., 2016). If prey refuge or predator attraction transpire in both space and time, the realized niche (Hutchinson, 1957) between predator and prey will be relaxed, and predation encounter rates may be reduced. This can lead to decreased predation rates, altered population dynamics, or phenomena such as mesopredator release (Crooks & Soulé, 1999).

2.3 | Human activity does not alter predator–prey overlap

Human activity may have no clear effect on the overlap among predators and prey, obscuring “winners” or “losers” in the predator–prey behavioural response race. This condition is likely to emerge when neither ecological player responds to human activity. Such lack of response could indicate at least four underlying mechanisms (Smith et al., 2021) including, but not limited to, high tolerance thresholds for human activity, perception of humans as non-threatening, intrinsic or extrinsic constraints on behavioural adjustments, and temporary transitions between avoidance and attraction. A true lack of response can only be measured when an animal does not alter its behaviour despite consistency in the density of competitors, predators, and resources across a human-use gradient. Because community composition also generally varies with anthropogenic disturbances (Ordeñana et al., 2010), fully characterizing the conditions underlying non-response to humans may require additional non-observational approaches, such as experiments (e.g. Suraci et al., 2019) or simulations (e.g. Thompson et al., 2018). Comparative studies of predator and prey spatiotemporal overlap in settings with and without human activity, or along gradients of human activity, may help to shed light on which behavioural pathways are most common. Such studies may also reveal whether functional traits, such as body size, influence an animal's behavioural response.

3 | CASE STUDY: MEASURING HUMAN INFLUENCE ON PREDATOR–PREY TEMPORAL OVERLAP

Our framework formalizes four behavioural pathways for how human activity may alter predator–prey overlap; yet, it remains important to test support for related hypotheses. To demonstrate how researchers can apply empirical data to our framework, we evaluated these four hypotheses in a literature review and analysis, and tested whether the behavioural response patterns were generalizable based on functional traits of each predator and its prey. We selected studies that measured temporal activity and overlap of predators and prey at paired settings of high and low human activity (for full Methods, see [Supporting Information](#)). Briefly, we limited our analysis to terrestrial mammals with a body mass >1 kg in line with recent research suggesting that medium and large-bodied terrestrial mammals exhibit varied responses to human activity (Frey et al., 2020; Suraci et al., 2021). We focused our review on published camera trap studies that reported predator–prey temporal overlap, given that the temporal dimension is often overlooked, more easily standardized than the spatial dimension, and is potentially more critical to predicting a predation event (Moll et al., 2017). In total, we reviewed 6646 abstracts and 405 papers to identify available data for 178 predator–prey dyads from 19 camera trap studies. These 19 studies spanned five continents and included forest, savanna, shrubland and desert ecosystems (see [Supporting Information](#)).

For each species in each study, we calculated the relative difference in the diurnal activity ratio (i.e. the proportion of daytime activity) at paired settings of high and low human activity. This calculation allowed us to visualize the difference between the temporal niche of each predator and its prey, relative to the diurnal human niche. Next, given that functional traits can influence an animal's perception of risk–reward cues, we tested whether functional traits (including prey order, body size, predator hunting mode, trophic level, predator guild and circadian rhythm) influenced the difference in diurnal activity of predator–prey dyads between paired settings of low and high human activity. Finally, to estimate how human activity altered the overlap between predator and prey, we calculated the difference in temporal overlap coefficients of predator–prey dyads between paired settings of low and high human activity (see [Supporting Information](#)).

We found evidence to suggest that mammalian predator–prey dyads respond to human activity in each of our proposed behavioural response pathways ([Figure 2a](#)). In settings of high human activity, 70 predator–prey dyads showed temporal patterns of mutual avoidance, while 60 exhibited prey refuge, 23 predator attraction and 19 mutual attraction to human activity. Six predator–prey dyads showed no change. Only half of the predator–prey dyads that exhibited mutual attraction (44%) and mutual avoidance (51%) increased temporal overlap with each other. Similarly only 49% of dyads exhibiting prey refuge and 27% exhibiting predator attraction decreased temporal overlap with each other in settings of high human use. Thus, temporal overlap did not consistently increase among predator–prey dyads exhibiting congruent activity shifts (i.e. mutual attraction to or avoidance of human activity), and likewise, temporal overlap did not consistently decrease among predator–prey dyads exhibiting divergent activity shifts ([Figure 2b](#)), as per our framework's expectations.

One explanation for why many predator–prey dyads had higher overlap with one another despite opposite responses to humans (i.e. prey refugia or prey switching; one ecological player becomes more nocturnal while the other becomes more diurnal) may be that human-avoidant prey can tolerate high overlap with a predator rather than tolerate high human activity (see Zbyryt et al., 2018). For instance, although black-tailed jackrabbits *Lepus californicus* had lower diurnal activity and bobcats *Lynx rufus* had higher diurnal activity in settings of high human activity, these species exhibited higher overlap with each other (see [Supporting Information](#); Baker & Leberg, 2018). More than 70% of the predator–prey dyads that exhibited predator attraction reflected this phenomenon. Thus, hypothesis testing within our framework can highlight differences in risk trade-offs for predators and their prey in settings of high human activity. Our analyses also revealed that some predator–prey dyads exhibited similar diel responses to human activity (i.e. mutual avoidance or mutual attraction; both predator and prey become more diurnal or nocturnal) yet decreased overlap with one another ([Figure 2b](#)). This finding may show maintenance of temporal partitioning between predators and prey at a fine scale, despite human-induced activity shifts (Ferreiro-Arias et al., 2021). For instance, while leopards *Panthera pardus* and spotted deer *Axis axis*

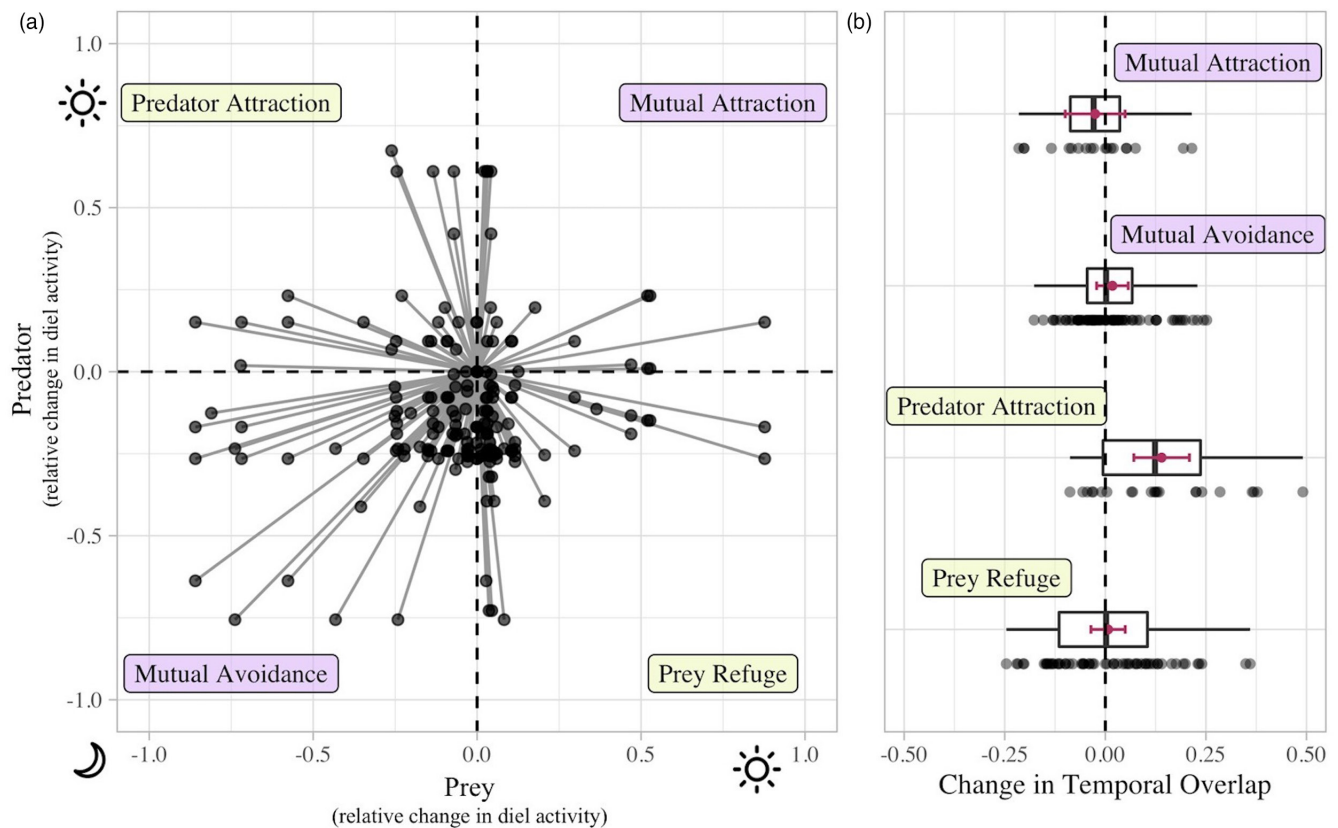


FIGURE 2 Human influence on predator–prey dyad (a) temporal activity and (b) temporal overlap based on review of camera trap studies between paired settings of low and high human use. (a) Lines reflect the relative magnitude and direction of the diel activity ratio toward nocturnality (−1) or diurnality (1) for each predator–prey dyad in paired settings of low to high human use ($n = 178$ predator–prey dyads, 19 studies) to indicate the behavioural response pathway (e.g. mutual attraction, mutual avoidance, prey refuge, predator attraction). (b) Black dots represent the change in predator–prey dyad temporal overlap (Δ) between paired settings of low and high human use, as grouped by corresponding behavioural response pathway ($n = 167$ predator–prey dyads, 16 studies). Red error bars represent estimated marginal means and $\pm 95\%$ confidence interval.

exhibited decreased diurnal activity to mutually avoid high human activity, spotted deer avoided human activity to a lesser degree, ultimately reducing overlap between spotted deer and leopards (see [Supporting Information](#); Carter et al., 2015). For prey, maintaining fine-scale spatiotemporal partitioning with both natural and human predators could come at the cost of altered stress and fecundity (Tuomainen & Candolin, 2011) or increased overlap among competitors (Manlick & Pauli, 2020; Sévêque et al., 2020; Smith et al., 2018). Ecological outcomes for these scenarios might include increased intraspecific competition (Carter et al., 2015; Wang et al., 2015) and resource limitation (Muhly et al., 2011), rather than increased predation encounter risk, as key drivers of population dynamics.

We found no effect of functional traits on the change in diurnal activity ratios for terrestrial mammal predators and prey between paired settings of high and low human activity (Figure 3; $n = 49$ predators, $n = 76$ prey, 19 studies). It is possible that the variability of human activity across the studies obscured underlying behavioural response patterns, especially given the relatively small number of studies ($n = 19$). It is also possible that in mammals, behavioural responses to humans are more strongly driven

by in-situ learning and experience than by the functional traits we tested. To examine these possibilities, researchers could use this framework to test how different types, magnitudes, and frequencies of human activity influence the behavioural response of the same predator–prey dyads. Similarly, researchers might consider whether morphology or past experience with humans drives the behaviour of the focal animals.

Future applications of this framework should ensure that change in animal activity and predator–prey overlap is measured relative to peak human activity. The published studies in our analysis exhibited diurnal human activity, but the peak impacts of human presence and infrastructure can also be crepuscular or nocturnal. For instance, lights or generators may turn on at night, or humans may tend agriculture at dawn and dusk, leaving fields unattended during the heat of the day. If the onset of peak human activity coincides with either a predator or prey's peak in activity, human impacts on predator–prey overlap may be greater.

While our analysis revealed that, in paired settings of high human activity, predator–prey activity resembled all four predicted behavioural pathways, such an analysis is incomplete without concurrent measures of animal responses in space and time. In our review,

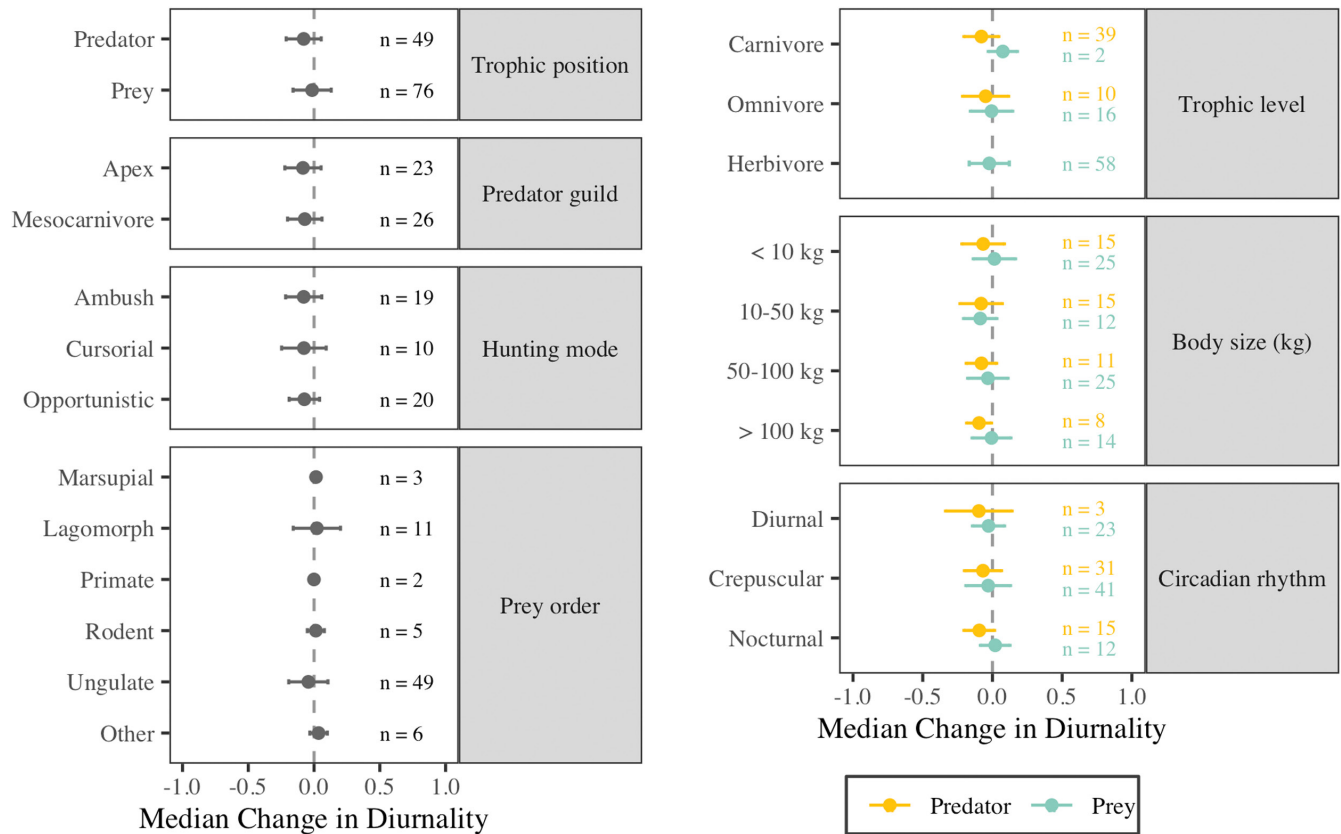


FIGURE 3 The influence of functional traits on the change in diurnal activity of terrestrial mammals, based on a review of paired camera trap studies. The change in diurnal activity ratio was calculated between paired settings of low and high human activity for each species in each study ($n = 49$ predators, $n = 76$ prey, 19 studies).

we found that studies seldom reported both temporal and spatial impacts of human activity on animal behaviour. Paired research designs that measured human impacts on both predators and their prey were similarly rare. Out of the 405 abstracts that warranted a full review, we excluded 155 studies that did not use camera trap array study designs, 75 studies for lacking concurrent data on mammal predators and prey, 80 studies that did not adequately distinguish between high and low human use, 28 studies that had fewer than 10 camera sites or did not include temporal data and 48 studies with temporal data in the wrong format for our analysis. We suggest researchers apply this framework to local empirical data to test for site-specific or species-specific patterns in both space and time.

4 | LINKING PREDATOR-PREY OVERLAP TO ECOLOGICAL OUTCOMES

Our framework (Figure 1) provides testable hypotheses regarding the influence of humans on predator-prey behaviour and overlap. However, the measurement of human impacts on predator-prey overlap is only a first step to identifying whether species interactions may change. Taken together, these concepts, as well as a few key considerations and additional empirical methods, can help researchers link human-altered predator-prey overlap to broader

ecological outcomes including predator diet, predation rates, competitive exclusion, trophic interactions.

Most importantly, it is difficult to infer how altered behaviour and spatiotemporal overlap influence predation encounter rate without accounting for differences in predator and prey population density. Predator consumption relies heavily on prey density (Holling, 1959; Solomon, 1949). Recent extensions of density estimation methods, such as the random encounter staying time model, can allow for robust estimation of animal density without individual recognition (Nakashima et al., 2018). However, such methods rely on accounting for variation in detection by study, site, survey design, or species, which can vary widely (Moll et al., 2020). To be considered robust, human-impact studies that link animal behaviour to predation would ideally collect data on a wide array of metrics, beginning with behavioural response as a first step but also including demography, density, and abundance.

Another key consideration in linking predator-prey overlap to ecological outcomes is that altered overlap of dyads may not predict where or when predation events occur (Suraci et al., 2022). Prey might continue to avoid predators at fine scales, maintaining spatiotemporal partitioning despite high overlap. In such cases, non-consumptive effects (i.e. stress that leads to lower fecundity) may emerge if prey employ energetically costly anti-predator behaviours to avoid both humans and predators (Frid & Dill, 2002; Soudijn et al., 2020). Pairing

multi-species behavioural studies with demographic or physiological studies will be needed to determine whether consumptive or non-consumptive effects of predation change as a result of human-altered predator–prey overlap (e.g. Zbyryt et al., 2018).

Measuring human impacts on animal responses at the appropriate scale can also be key to accurately identifying ecological outcomes of behavioural shifts. Conceivably, predators and prey may respond to different human stimuli (including various auditory, olfactory and visual cues), and at different scales. This can lead to situations where one species may be attracted to human activity at a broad spatial scale (e.g. to forage on anthropogenic food sources), but both predator and prey avoid humans at fine spatial scales (e.g. Rogala et al., 2011). When possible, studies that measure animal behaviour across spatio-temporal scales will be most informative. When this is not feasible, researchers might consider how the goal of the study and the ecology of the system correspond to trade-offs associated with choosing various sampling designs (e.g. see Steidl & Powell, 2006).

Comprehensive assessments of human influence on predator–prey interactions consider both spatial and temporal dimensions of predator–prey overlap, because prey may avoid predators in one dimension (i.e. space or time) despite high overlap in another dimension. If human activity increases predator–prey overlap in space, prey may still safely exploit risky places by foraging during predator downtimes (Beauchamp, 2007), though non-optimal foraging times may be energetically costly to prey (Kronfeld-Schor & Dayan, 2003). Methods like GPS telemetry and camera trapping facilitate inference on both spatial and temporal distribution simultaneously. Furthermore, using indices that simultaneously estimate predator–prey overlap in space and time, such as occupancy models with a continuous-time detection process (Kellner et al., 2022) or Bayesian time-dependent observation models (Ait Kaci Azzou et al., 2021), can avoid these issues and provide more accurate estimates of human impact on encounter probabilities. Applying our proposed framework to such inferences would provide a rigorous test of how humans influence predator–prey outcomes across dimensions.

As humans modify the contest between predators and prey, complex feedbacks among multiple players can obscure the true mechanisms driving an observed pattern. Human activity can influence each ecological player, while predator and prey simultaneously influence each other. As a result, it is often difficult to disentangle, for instance, whether a prey refuge pattern is the consequence of (a) prey attraction to human activity, or (b) prey exploitation of a predator-free zone. To resolve these types of uncertainty, researchers may consider using additional controlled experiments to further isolate and test the hypothesized drivers of an observed response to human activity (e.g. Sarmiento & Berger, 2017).

While our framework explicitly considers predator–prey relationships as dyads, rarely are predators and prey in obligate pairings. Human activity may influence prey choice, for example, when predators have multiple prey, or reshape multi-predator effects on prey with more than one predator (Sih et al., 1998). To advance predictions of how human activity will affect species interactions, it will be beneficial to apply this framework to combinations of predators,

prey, and competitors (Mills & Harris, 2020). One promising avenue of research lies in comparing how species richness, composition, and food web structure influence predator–prey responses to human activity (e.g. see Sévêque et al., 2020). Researchers can deploy these research designs to identify whether predators, prey, competitors or human disturbance are driving the predominant patterns of dietary preference and predation rate.

Future research might consider further investigation into how human influence on predator–prey overlap, encounter or predation, is linked to the functional traits (e.g. body size, hunting mode, circadian rhythm) of each interactor. For instance, nocturnal prey may outperform diurnal human-avoidant predators forced to hunt at night, limiting encounter risk despite high overlap between predator and prey (Beauchamp, 2007). One successful approach to clarifying whether altered overlap results in altered predation is using multi-species camera trap studies in tandem with diet composition studies (e.g. Smith et al., 2018). Pairing camera and diet data can allow researchers to connect overlap to predation non-invasively, avoiding the more costly and effort-intensive research designs that use GPS telemetry clusters and animal necropsy data to estimate predation.

In certain cases, human influence on predator–prey overlap may be temporary and without lasting consequences for ecological communities. For instance, if predators and prey habituate to human activity over time (Blumstein, 2016), encounter rates may be maintained, and the predator–prey response race may continue unaltered by humans. Yet in this case, the rise of human-wildlife conflict and use of lethal or non-lethal deterrents may in turn affect animal behaviour and predator–prey overlap (Manlick & Pauli, 2020). Researchers can use iterative experiments that measure how multiple ecological players habituate or sensitize to human disturbance (e.g. Uchida & Blumstein, 2021) to better capture which of the four possible human-induced response pathways predict shifts in encounter risk over time.

Identifying thresholds of human activity that alter animal behaviour will be key to drawing useful inference from human impact studies and improving our understanding of when altered interactions may have reverberating impacts across ecosystems. Examples of such studies include comparison of animal response to motorized versus non-motorized recreation (Larson et al., 2016), leashed versus unleashed domestic dogs (Reed & Merenlender, 2011), exurban versus suburban development (Merenlender et al., 2009; Smith, Duane, & Wilmers, 2019), dense versus dispersed oil development (Sawyer et al., 2020), and the influence of human presence versus the human footprint (Nickel et al., 2020; Suraci et al., 2021). Such measurements can aid in creating specific guidelines for human activity near wildlife. Ultimately, these research designs will help anticipate how predators and prey respond to human activity in rapidly changing landscapes.

5 | CONCLUSIONS

Behavioural ecology is increasingly recognized as a valuable aspect of population and ecosystem management (Gaynor

et al., 2021), yet complex behavioural interactions among predators, prey, and humans (Kuijper et al., 2016) challenge the application of theory to practical solutions. Nonetheless, understanding species interactions remains key to the coexistence and persistence of wildlife, and ecosystem function, in settings with high human activity. For example, anthropogenic effects on prey may sometimes need to be minimized before predator recovery and predator-prey interactions can be restored (Lahkar et al., 2020). Unfortunately, the daunting task of studying or modelling complex behavioural feedbacks among players in this ecological game has deterred progress in understanding the ecology of landscapes characterized by high human activity. Investment in models that explain how humans modify species interactions, rather than solely species richness or abundance, is critical to fundamental ecology and the implementation of science-based management and conservation practice. Adopting our framework can help researchers test for patterns of human influence on strongly interacting species and identify possible mechanisms driving broader ecological outcomes.

AUTHOR CONTRIBUTIONS

Amy Van Scoyoc conceived the framework in conversation with Justine A. Smith and Justin S. Brashares. Amy Van Scoyoc, Justine A. Smith, Kaitlyn M. Gaynor and Kristin Barker conducted the literature review. Amy Van Scoyoc analysed the data and led the writing of the manuscript. Justine A. Smith, Kaitlyn M. Gaynor, Kristin Barker and Justin S. Brashares contributed critically to the interpretation of results, drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

A list of data sources used in the study are provided in the Data sources section. The authors confirm that any data that was not available from published sources was used and cited with permission of the data's original authors. Data used to produce Figures 2 and 3 are available from the Dryad Digital Repository <https://doi.org/10.6078/D1FQ42> (Van Scoyoc et al., 2023).

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DATA SOURCES

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SUPPORTING INFORMATION

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

Table S1. Site descriptions, human activity level, and method used to calculate predator-prey activity ratio and overlap coefficient of each study in analysis (n = 19).

Table S2. Summary of predator and prey activity ratios at high and low human use for 19 studies and 178 predator-prey dyads.

Table S3. Summary of predator and prey overlap coefficients at high and low human use for 17 studies and 172 predator-prey dyads.

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